Aplacophora as Progenetic Aculiferans and the Coelomate Origin of Mollusks as the Sister Taxon of Sipuncula[1]

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Abstract. Evidence is presented in support of the following phylogenetic hypotheses: (1) Sipuncula are the sister taxon of Mollusca; (2) the two aplacophoran taxa, Neomeniomorpha (= neomenioids) and Chaetodermomorpha (= chaetoderms), are monophyletic with a common neomenioid-like ancestor, and of the two taxa, Chaetodermomorpha are more derived; (3) Aplacophora and Polyplacophora are sister taxa and form a clade, Aculifera; (4) Aculifera are the sister group of the remaining extant mollusks, Conchifera; and (5) Aplacophora are progenetic Aculifera.

The evidence is based on homologies of early and late embryological development, adult morphologies, and molecular analyses. Embryological development in sipunculans and mollusks shows a close relationship between them, and embryological development of the shell separates Aculifera and Conchifera. Adult morphologies indicate: (1) monophyly of Aplacophora; (2) sister-group relationship between Aplacophora and Polyplacophora; (3) a molluscan plesiomorphy of nonsegmented serial replication of organs; and (4) progenesis in Aplacophora. Molecular evidence supports the embryological and morphological relationships between Sipuncula and Mollusca.

Mollusca are thus hypothesized to be coelomate Eutrochozoa, which share an ancestor that probably had serial replication of organs. Differences in size and structure of the coelom among Eutrochozoa are hypothesized to have been brought about by changes in the timing and the process of cavitation of the mesodermal bands that arise from cell 4d. Through the process of progenesis Aplacophora retained an ovoid embryological shape and several internal structures that, although they appear to be in a primitive state, are actually secondarily derived as is quadrant D specification during early cleavage.

Introduction

The uniqueness of Aplacophora among Mollusca lies in their derived vermiform body in combination with an internal organization that appears to reflect a primitive molluscan state, especially the simple ladderlike nervous system, serial musculature, distichous radula (two teeth per row) in its plesiomorphic aplacophoran state, simple digestive system, and epidermis that produces an aculiferous cuticle. Their evolutionary significance to the phylum has long been a matter for conjecture. First came the question of whether Aplacophora were even mollusks, as they lack a number of "typical" characters such as a shell, mantle, and kidneys (*e.g.*, Thiele, 1902; H. Hoffmann, 1929-30), but they have more usually been considered to belong within the phylum because of similarities to chitons in their nervous system (Amphineura) and spicules (Aculifera) (*e.g.*, Spengel, 1881; Heath, 1911). Further discussions were concerned with whether aplacophorans were "degraded" or truly "primitive" mollusks (see Hyman, 1967, pp. 68–70 for a historical account).

There have been no current arguments which separate Aplacophora from Mollusca since evidence for a close relationship between Aplacophora and Polyplacophora was published by S. Hoffman (1949), but under present discussion is their origin and position within the phylum (Salvini-Plawen, 1972, 1981a, 1985; Scheltema, 1978, 1988), as well as the origin of the phylum Mollusca itself. Mollusca have been argued either to have a noncoelomate origin and to be the sister taxon of the eucoelomate Annelia-Echiura-Sipuncula (Salvini-Plawen, 1972, 1985 fig. 42), or to be eucoelomates with an ancestor in common

with other coelomates (Wingstrand, 1985; Scheltema, 1988). In either argument, Aplacophora have been considered stem forms and therefore preceded the Monoplacophora with serial replication of organs.

Hypotheses for a noncoelomate origin rest on the argument that the worm-like Aplacophora with replicated lateroventral musculature evolved from a turbellariomorph ancestor, and that consequently the molluscan coelom is not homologous to that in the Eutrochozoa. A coelomate origin has been hypothesized from annelid-mollusk relationships, including the presence of a cell 4d that gives rise to mesoblasts and consequently a homologous coelom, the presence of a trochophore larva, and serial repetition of body parts. Because the molluscan coelom is small and unsegmented, the idea that annelids and mollusks form a clade with a common segmented ancestor is poorly accepted. The dichotomous choice between either a turbellariomorph or an annelid-like ancestor for mollusks has dominated recent thinking about molluscan evolution (*e.g.,* Hyman, 1967; Haszprunar, 1992), and the relationship of mollusks to other Eutrochozoa has not been examined. However, recent molecular data discussed below urge reconsideration of molluscan relationships to other phyla.

Evidence is presented here to support the hypotheses that (1) Mollusca are eucoelomates with their closest living relatives in Sipuncula, their sister group; (2) Aplacophora and Polyplacophora are sister groups in the subphylum Aculifera (contradicting Scheltema, 1978, 1988); (3) Aculifera are the sister group of the remaining living mollusks, Conchifera; (4) the aplacophoran taxa Chaetodermomorpha (= Caudofoveata, here also called chaetoderms) and Neomeniomorpha (= Solenogastres sensu nomine Salvini-Plawen, here also called neomenioids) are monophyletic, sharing a neomenioid-like ancestor; and (5) aplacophorans are progenetic Aculifera. Considered in the discussion is the homology of the eutrochozoan coelom and the evolutionary difference between metamerism, or segmentation as it occurs in the annelids, and serial replication of organs, as found in *Neopilina* and *Vema* (Wingstrand, 1985). The term "metamerism" is used here only to denote a segmented coelom; "serial replication" is used to denote the more general case of serial repetition of organs, whether or not by metameres.

Evidence that Mollusca are Descended from Coelomates

Mollusca have a coelom consisting of gonadal lumina, pericardium, and kidneys, as well as part of the gametoducts in Aplacophora. A noncoelomate ancestry calls for the widening of a pericardial space lined by mesoderm as protection for a heart (Salvini-Plawen, 1968a, 1972; not discussed 1985, 1990) and for gonads separate from the pericardium. This development of coelomic spaces would be a molluscan apomorphy, not homologous with annelid or sipunculan coelom. Alternatively, the molluscan pericardium can be considered as reduced from a large coelomic space homologous to that in other eutrochozoa. The involvement of the pericardial coelom in excretion is unique to mollusks. Ultrafiltration of blood occurs through podocytes that are present in most molluscan classes including Aplacophora (Andrews, 1988; Reynolds and Morse, 1991).

Five independent lines of evidence indicate that reduction of coelom is the case, and that Mollusca are eutrochozoan coelomates: (1) presence of the molluscan cross in mollusks and sipunculans and (2) homology of certain characters in larvae of mollusks and sipunculans indicate that mollusks and sipunculans are sister taxa; (3) a large pericardium among "primitive" mollusks indicates that it is a molluscan plesiomorphy; (4) the embryological development of mesoderm in annelids, mollusks, sipunculans, and nemertines is similar, and the coelom in the four groups is homologous; and (5) molecular data groups mollusks with other eutrochozoans.

Sipunculans as sister taxon of the mollusks

An evolutionary relationship between sipunculans and mollusks lies in their early embryological development and in morphological features of sipunculan pelagosphera and molluscan larvae.

Molluscan cross. The molluscan cross is found in the embryological development of Gastropoda, Polyplacophora, Scaphopoda, and Aplacophora by the end of the 64-cell stage (Verdonk and van den Biggelaar, 1983; Heath, 1899; van Dongen and Geilenkirchen, 1974; Baba, 1951). It is formed by $1a^{12}$–$1d^{12}$ cells and their descendents, with cells $1a^{112}$–$1d^{112}$, called peripheral rosette cells, forming the angle between the arms of the cross (Fig. 1A, B, D, peripheral cells solid black). In Annelida, however, it is cells $1a^{112}$–$1d^{112}$ that form the cross (Fig. 1E, cross cells solid black) (Wilson, 1892). In the 64-cell stage of the neomenioid aplacophoran *Epimenia verrucosa* figured by Baba (1951), a molluscan cross seems apparent from Baba's shading (Fig. 1D), although Salvini-Plawen (1985) found "no definite cross formation" in the same source. Manuscript drawings by G. Gustafson of developing *Chaetoderma nitidulum* eggs likewise show a molluscan cross. In contrast to most mollusks, early cleavage in Pelecypoda is asynchronous and bilateral, and no cross is formed; its absence would seem to be an apomorphy. Likewise, development in Cephalopoda seems an apomorphy of that group, which has telolecithal eggs, early bilateral cleavage, and no molluscan cross.

In Sipuncula, a molluscan—not an annelid—cross is formed, as Rice (1975, 1985) has emphasized and refigured from Gerould (1906), who first described its presence
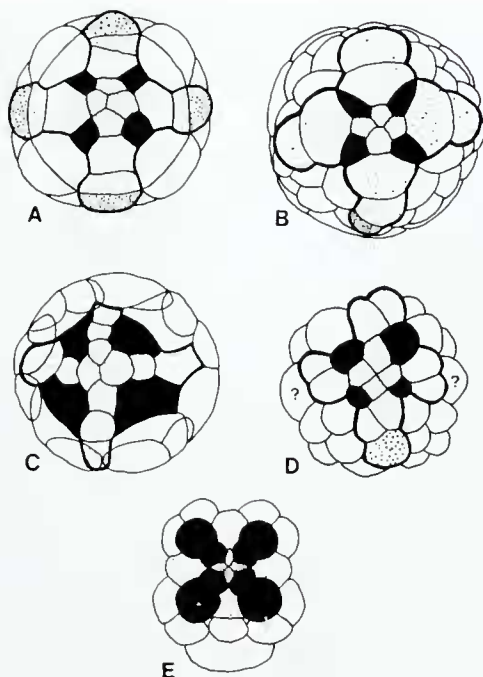
Figure 1. (A-D) The molluscan cross. (A) Gastropoda (*Lymnaea stagnalis*, after Verdonk and van den Biggelaar, 1983, p. 111 fig. 3b); (B) Polyplacophora (*Stenoplax heathiana*, after Heath, 1899, pl. 32, fig. 23); (C) Sipuncula (*Golfingia vulgaris*, after Gerould, 1906, p. 99, fig. D, as published in Rice, 1975, p. 99, fig. 17); (D) Aplacophora (*Epimenia verrucosa*, after Baba, 1951, p. 46, fig. 18). The apical rosette $1a^{111}-1d^{111}$ is shown in fine, close stippling; arms of the cross $1a^{12}-1d^{12}$ and daughter cells are shown in fine, open stippling; tip cells of cross $2a^{11}-2d^{11}$ are shown in coarse stippling; peripheral rosette cells $1a^{112}-1d^{112}$ are solid; and trochoblast cells $1a^2-1d^2$ are clear. In *Epimenia* (D), the cleavage stage appears to be earlier than shown in A-C, as the tip cells have not yet separated from $2a^1$ and $2c^1$ (indicated by question marks), and the arms of the cross are not quite straight, similar to an earlier stage in Polyplacophora (Heath, 1899, pl. 32, fig. 17). In B, only one tip cell was discernible in Heath's illustration, and in C tip cells were not indicated in Gerould's original figure. (E) Annelid cross, Polychaeta (*Nereis*) (after Wilson, 1892, p. 396, diagram II). The apical rosette $1a^{111}-1d^{111}$ is shown in fine, close stippling; peripheral cells $1a^{12}-1d^{12}$ are shown in fine, open stippling; and the arms of the cross from $1a^{112}-1d^{112}$ are solid.

in sipunculan development (Fig. 1C). The presence of a molluscan cross during embryological development is understood here to be of phylogenetic importance, and sipunculans and mollusks share a character not found in either annelids or flatworms (Freeman and Lundelius, 1992). Its presence can be considered apomorphic to the embryonic morphology of turbellarians, which lack a cross.

Similarities between sipunculan and molluscan larvae. Gerould (1906) noticed certain other resemblances to mollusks besides the molluscan cross in the development of sipunculans. In particular, he found similarity between sipunculan pelagosphera and molluscan larvae. The pelagosphera is unique to sipunculans. It is a swimming larva

that metamorphoses from a trochophore stage (Rice, 1975, 1985). Gerould noted the resemblance of the pelagosphera lip glands to chiton larval pedal glands, and of the pelagosphera buccal organ to the radula sac in chiton larvae (Figs. 2, 3, 4). Pelagosphera larvae can either swim upright with the large metatroch or creep, head-down, along a solid surface. These activities are lost along with the larval head at metamorphosis. Jägersten (1963) first described creeping in living pelagosphera, and he related it to a creeping gastropod. He also noted that the buccal organ (= pharyngeal bulb, Schlundkopf) was used in feeding. Later Jägersten (1972) proposed a possible, but not certain, homology of the pelagosphera lip, which is the creeping surface posterior to the mouth, and the creeping lobe, or foot, between mouth and anus of molluscan larvae.

Rice (1975, pp. 120–121) described the creeping locomotion of pelagosphera as follows: "The larva is able to . . . glide along with . . . [the] head flattened against the bottom. Frequently the larvae . . . may crawl in the manner of an inchworm, presumably scraping material from the bottom. The continual eversion of the buccal organ during feeding probably aids in the removal of food from the substratum. This tough muscular organ [covered by cuticle, Rice, 1973] is believed to function in breaking up material into small particles for feeding. . ." A mucuslike substance from the lip glands is secreted as the animal moves along a natural substratum (Rice, 1981 and pers. comm.). My own recent observations on living pelagosphera corroborate many of Rice's.

Precise descriptions of the protrusible buccal organ and lip gland have been given by Rice (1973). The buccal organ is a muscular sac, ventral and posterior to a cuticle-lined invagination called the buccal groove that lies below the esophagus. The epithelium of the buccal organ is overlain by the cuticle of the ventral side of the buccal groove and is the area first protruded (Fig. 2). Although the precise innervation of the buccal organ was not demonstrated, the circumesophageal connectives, which arise from the dorsal cerebral ganglion, are closely associated with the organ. Both the topography and function of the buccal organ and groove are remarkably similar to those of the radular apparatus in mollusks: ventral odontophore = buccal organ; ventral radula sac = buccal groove; and ventral cuticular radula = ventral portion of the cuticular buccal groove. Furthermore, the odontophore and probably the buccal organ are innervated through connectives united with the cerebral ganglion. The homology would be more certain if it were known whether the buccal organ musculature is formed from mesoderm, as is the odontophore of mollusks (Raven, 1966), or whether it is myoepithelial as in archiannelids (Jägersten, 1947; Rice, 1973).

The lip gland takes several forms in various pelagosphera, from a bilobed to a paired or four-lobed body
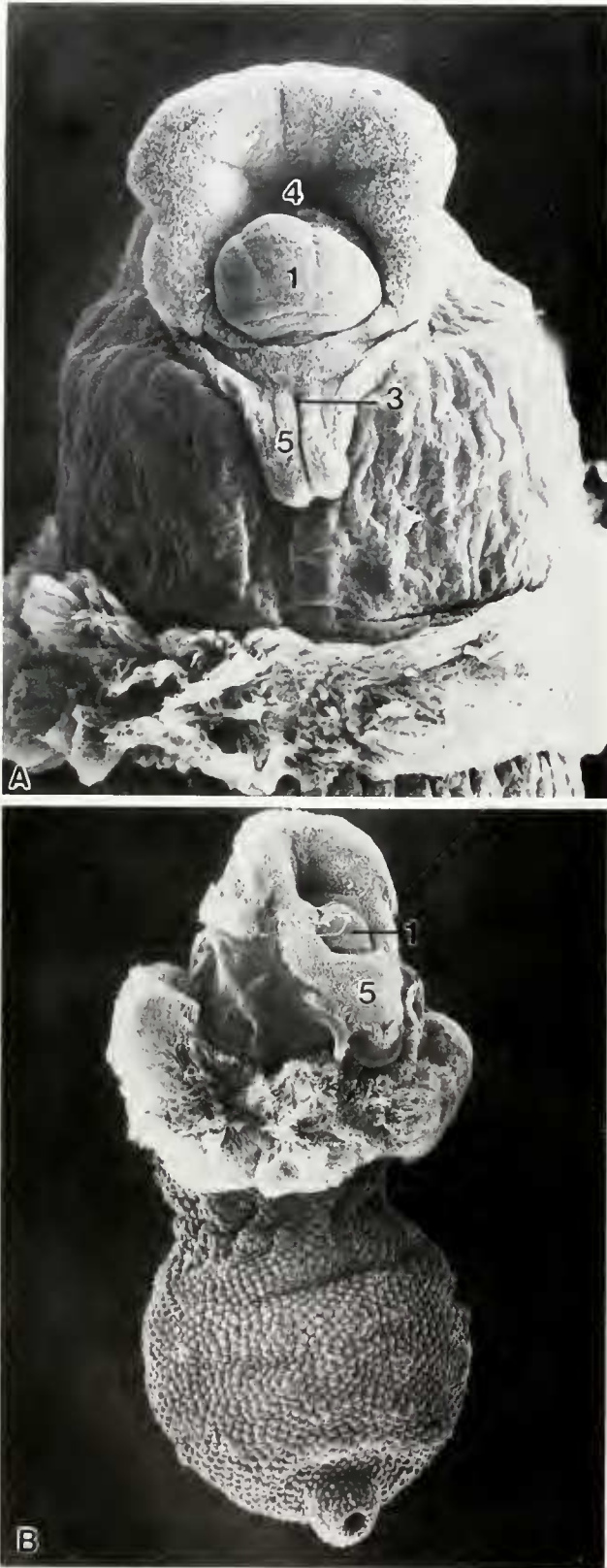
Figure 2. Pelagosphera larvae of Sipuncula. (A) Frontal view of head, *Sipunculus* sp. (from Rice, 1981, fig. 4). (B) Entire larva, *Aspidosiphon* sp. (from Rice, 1981, fig. 6). Numbers as in Figure 3: 1 buccal gland, 3 pore of lip gland, 4 mouth, 5 lip.

which opens either directly, or by way of a ciliated duct or ducts, into the lip pore. In comparison, the anterior pedal gland in larval chitons and in Aplacophora is ductless (*cf.,* Figs. 2A, 4B, 6C). Aplacophora, but not chitons, have a central ciliated pit.

Similarities in form and function in these three structures—lip and foot, lip glands and pedal glands, and buccal organ and radula with its sac—are striking. Their morphologies are particularly clear in sagittal sections of a pelagosphera and a chiton larva (Figs. 3, 4). There are also similarities in their development, as they all arise from posttrochal ectoderm, with these differences: in sipunculans, the origin of all three structures is stomodeal, whereas in mollusks, the ventral somatic plate, usually from cell 2d, gives rise to the foot and its glands, and only the radula sac is stomodeal (Raven, 1966). In Sipuncula as well, cell 2d gives rise to the somatic plate, which forms the ectoderm of the trunk (Rice, 1976). In mollusks, however, the proximity and functional interdependence of the somatic and stomodeal structures are indicated by the pedal contribution to feeding in veliger larvae. An anterior, medial ciliary tract is formed on the foot by which particles unsuitable for ingestion are rejected (Moor, 1983).

Only the head region of the pelagosphera, which is radically altered during metamorphosis to a juvenile sipunculan, can be compared to the Mollusca. The posterior part of the body with its large coelomic sac, nephridia, mid-dorsal anus, and ventral nerve cord, are already definitive adult structures.

Evidence from the presence of the molluscan cross and from locomotary and feeding structures that are similar in mollusks and larval sipunculans is sufficiently strong that the two phyla can be considered as sister groups, and mollusks, therefore, as eucoelomates. Of course, if the primitive mode of sipunculan development should prove to be by way of a nonfeeding, lecithotrophic larva, then the similarities between planktotrophic pelagosphera and molluscan larvae would be convergent. However, Rice (1985) most recently considered evolutionary questions of sipunculan larval development and concluded that a yolky egg and short-lived planktotrophic pelagosphera was the primitive mode of development.

Other considerations. Two further observations can be made to support arguments for a sipunculan-molluscan sister relationship, one embryological, the other paleontological. The first is the embryological development of Echiura (Newby, 1940) compared to that of the sipunculans. Echiurans have traditionally been linked with sipunculans, both having worm- or sac-like, unsegmented coelomate bodies, but echiurans afford a contrast to sipunculans in their closer relationship to annelids. They have an annelid cross rather than a molluscan cross during early cleavage, and as in annelids, the major ciliary band
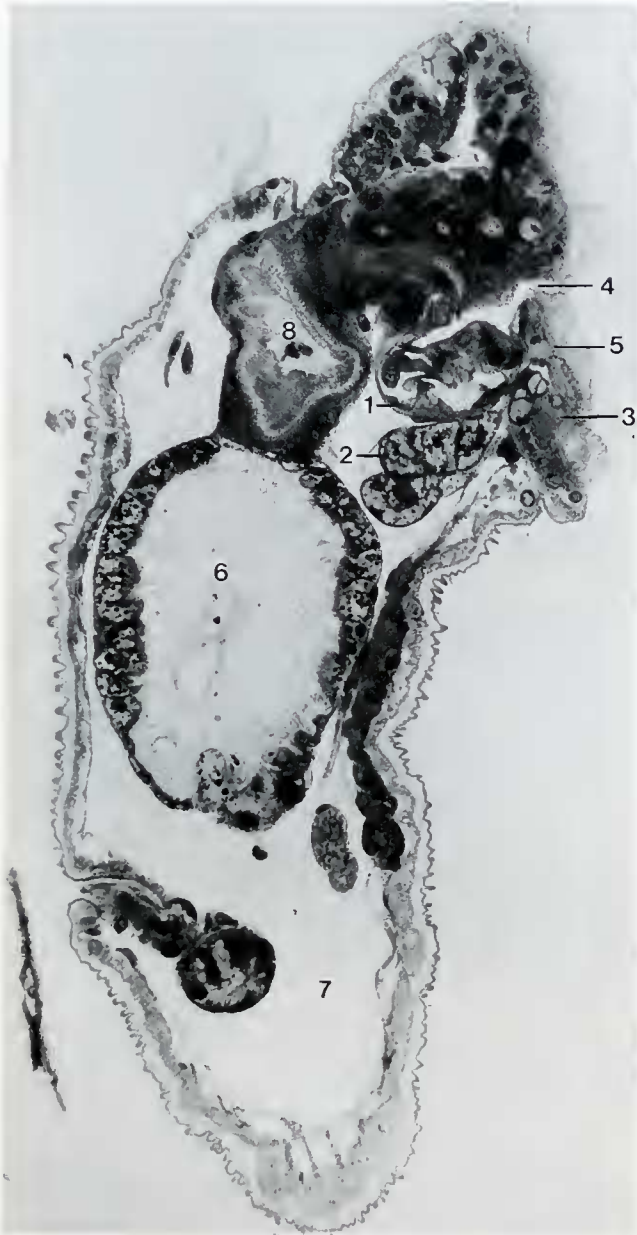
Figure 3. Midsagittal section of the pelagosphera larva, *Phascolosoma agassizii* (from Rice, 1973, pl. 5). 1 buccal organ, 2 lip gland, 3 pore of lip gland, 4 mouth, 5 lip, 6 stomach, 7 coelom, 8 esophagus.

of older echiuran larvae is the prototroch anterior to the mouth. In sipunculan pelagosphera, the metatroch below the mouth, not the prototroch, is the major swimming organ. Indeed, the region in pelagosphera that forms the head with its locomotory lip, lip gland, and buccal organ, is represented in echiuran larvae by only a few rows of cells between the prototroch and metatroch, and no larval organs are present.

If sipunculans are sister taxon of the Mollusca, they must have arisen, like mollusks, early in the evolution of

metazoans. One piece of evidence for an early sipunculan history is the mid-Cambrian genus *Ottoia* from the Burgess Shale. Considered priapulids by Conway Morris (Whittington, 1985) and close to priapulids by Banta and Rice (1976), the genus indicates great diversity of specialized sacciform, coelomate or pseudocoelomate, wormlike animals already in the early Paleozoic. Sipunculans therefore could have a very long, but unobservable and unverified, geologic history. A second piece of evidence is that sipunculans contain hemerythrins, found also only in priapulids, lingulid brachiopods, and some annelids (Curry and Runnegar, 1990). Because lingulids and probably priapulids and annelids are known from the early Cambrian, the presence of hemerythrins indicates a very long history for all forms having these oxygen transport molecules.

Size of the pericardium in "primitive" mollusks

The pericardium is larger relative to the heart in Aplacophora, Monoplacophora, and Polyplacophora than it is in Gastropoda, Pelecypoda, and Cephalopoda (Scheltema, 1973, 1988; Scheltema and Kuzirian, 1991) (Figs. 5, 6A). Ontogenetically, the pericardium is already large before the heart develops from pericardial epithelium in Aplacophora (Baba, 1938), and in Polyplacophora development of the pericardium precedes development of the gonad (Hammersten and Runnström, 1925). Thus the polarity of pericardial size is from large to small in Mollusca, and the continued reduction within the phylum is considered to be a derived condition of the Mollusca.
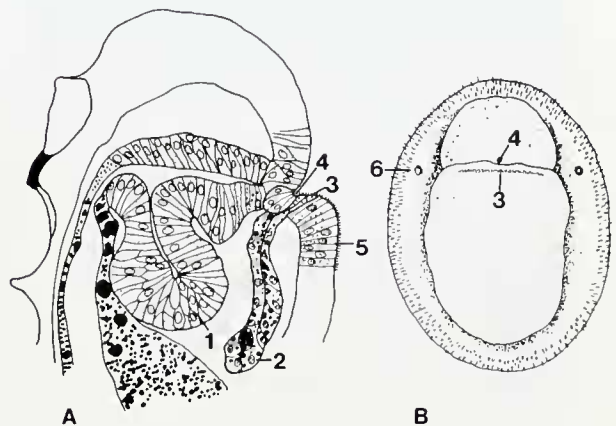

Figure 4. Newly settled larvae of Polyplacophora. (A) Midsagittal section of *Acanthochiton discrepans* (after Hammarsten and Runnström, 1925, fig. E, figure reversed). (B) Ventral view of *Stenoplax heathiana* just after metamorphosis (after Heath, 1899, fig. 59). The opening of the pedal gland (3) lies posterior to the mouth (4); the gland opens through "a series of . . . intercellular channels" rather than a duct (Heath, 1899, p. 631); compare with Figure 6C. 1 radula sac, 2 anterior pedal gland, 3 opening of pedal gland, 4 mouth, 5 foot, 6 larval eye. Structures numbered 1–5 are homologous to structures with the same numbers in Figs. 2, 3.
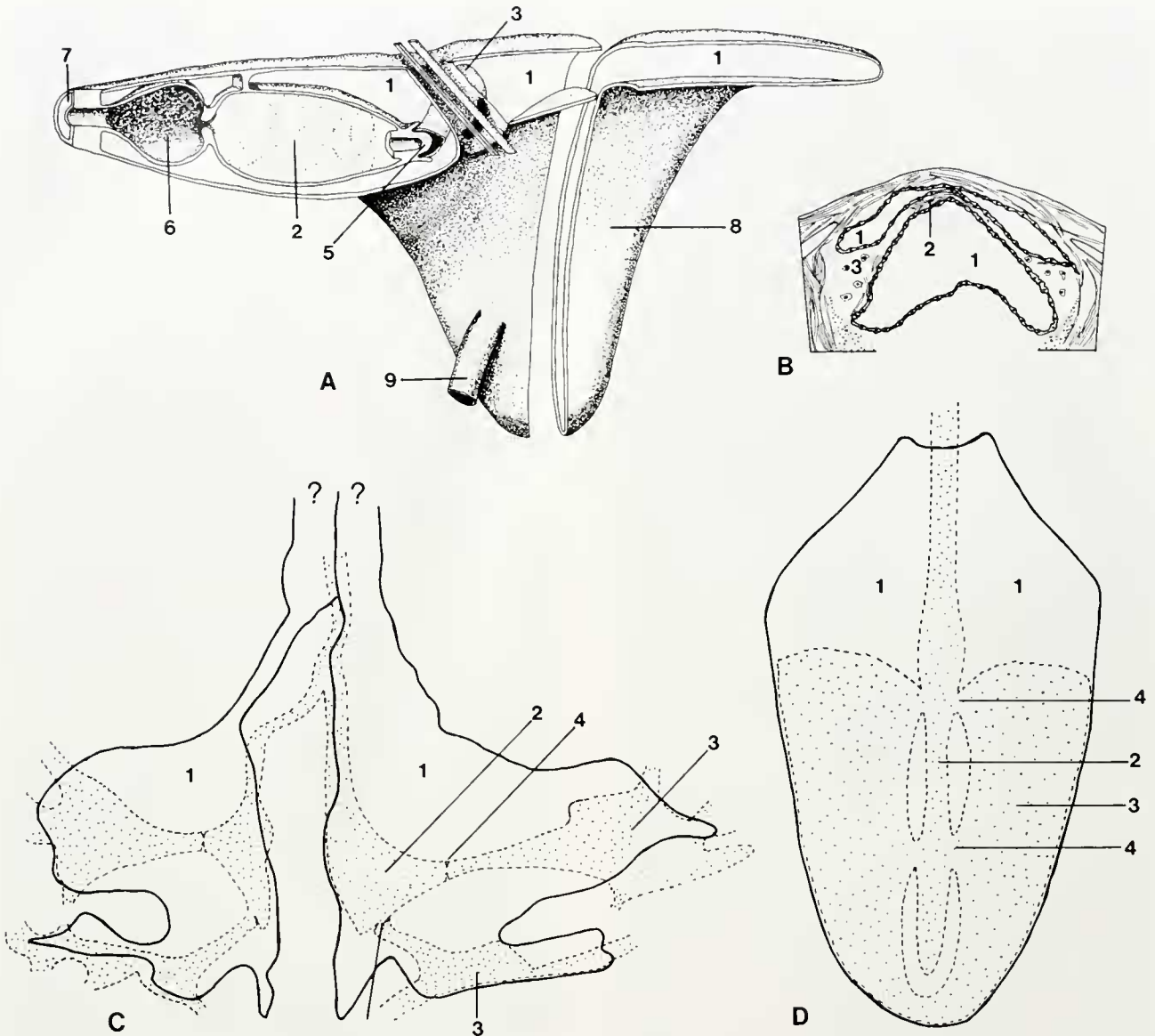
Figure 5. Large pericardial space and heart in primitive molluscs. (A) Aplacophoran, *Chaetoderma nitidulum,* sagittal section. Gametes pass from the gonads through the pericardium with its large, paired, lateral extensions ("horns") and thence into gametoducts leading to the mantle cavity (from Scheltema, 1973, fig. 2, and Scheltema, 1988, fig. 13). (B) Polyplacophoran, *Chiton sinclairi,* cross section (after Wissel, 1904, pl. 24, fig. 49). (C) Monoplacophoran, *Neopilina galathea,* dorsal view, with paired pericardial sacs, paired ventricles, and two pairs of auricles (after Lemche and Wingstrand, 1959, from Scheltema, 1988, fig. 13). (D) Polyplacophoran, *Acanthopleura echinata,* dorsal view, with two pairs of openings between auricles and ventricle (after Plate, 1898, from Scheltema, 1988, fig. 13). 1 pericardium, 2 ventricle, 3 auricle, 4 opening between auricle and ventricle, 5 auriculoventricular valve, 6 aortal bulb, 7 gonopericardial duct, 8 lateral extension of pericardium, 9 gametoduct.

Development of mesoderm

The interpretation that the coelom is reduced in Mollusca assumes that the molluscan pericardium is homologous to the coelom in other spiralian coelomates, namely Annelida and Sipuncula. In all three, the coelom is formed from mesoderm that originates from embryonic cell 4d. This cell gives rise to a pair of mesodermal teloblasts, which migrate inward to a ventrolateral position, one on each side of the midline (Verdonk and van den Biggelaar, 1983; Anderson, 1973; Rice, 1975) and proliferate forward into two lateral mesodermal bands. Mesodermal bands
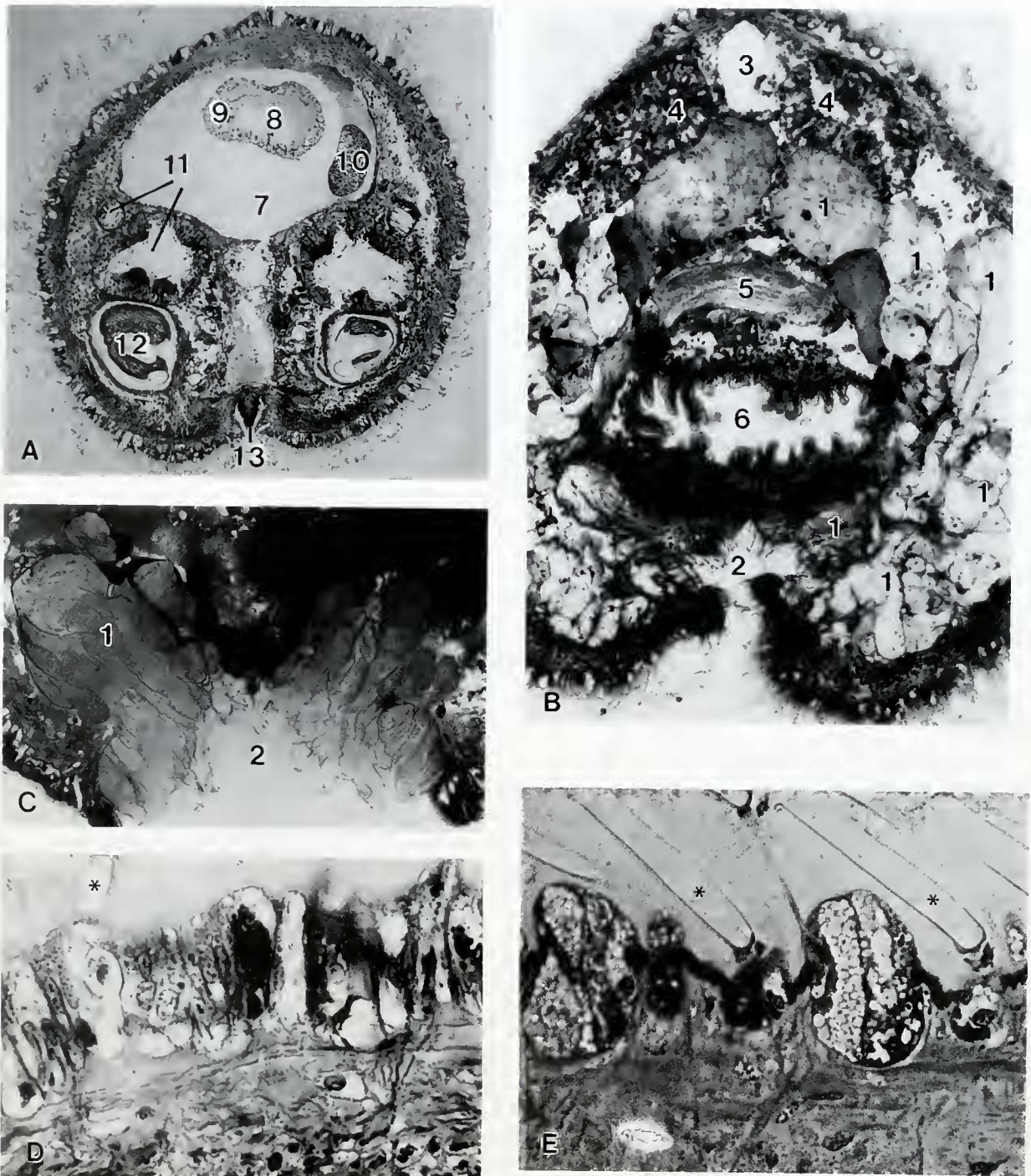
Figure 6. (A) Cross-section through the pericardium of a neomenioid aplacophoran, *Helicoradomenia juani* (from Scheltema and Kuzirian, 1991, fig. 5C). (B) Cross-section through the pedal gland and pedal pit of a neomenioid aplacophoran, *Ocheyoherpia* sp. The voluminous pedal gland occupies most of the head region; the lobes of the gland are in varying stages of secretion. (C) Ciliated pedal pit of *Helicoradomenia juani*. The pedal gland discharges into the pedal pit, not through distinct ducts, but through numerous channels as described for chitons (Fig. 4B). (D) Secretory epidermal papillae of the neomenioid aplacophoran, *Helicoradomenia juani* (from Scheltema and Kuzirian, 1991, fig. 2C). (E) Secretory epidermal papillae of the polyplacophoran, *Acanthochiton fascicularis* (from Fischer *et al.*, 1980, fig. 3). 1 pedal gland, 2 ciliated pedal pit, 3 dorsal blood sinus, 4 dorsal cecum of midgut, 5 cerebral ganglion, 6 oral cavity, 7 pericardium, 8 auricle, 9 ventricle, 10 ovum, 11 U-shaped gametoduct, 12 copulatory spicule pocket, 13 foot. Asterisks in D and E, cavities of dissolved spicules.

are present as well in Nemertini (Turbeville, 1986). In annelids, sipunculans, and nemertines, the coelom is formed by cavitation (schizocoely) of the bands. The coelom constitutes the major body cavity in annelids and sipunculans, but in nemertines it forms only vessels for blood circulation (Turbeville, 1986). In mollusks, the mesodermal bands break up into masses of coelenchyme, from which is formed a solid anlage or pair of anlagen that cavitate to form the pericardium, heart and kidneys (Raven, 1966; Moor, 1983). In some mollusks with paired anlagen, the pericardium begins as paired cavities before becoming united (Raven, 1966). In *Neopilina* the pericardium is still paired (Fig. 5C), and the large pericardial "horns" in some Aplacophora (Fig. 5A) may reflect an ancestral paired condition.

The coelom among the spiralian protostomes described here is interpreted as being homologous because of similarities in early embryological development. Differences in coelom formation among the four phyla apparently arise from variations in the timing of cavitation after the mesodermal bands have formed; but the differences in process are not considered sufficient to deny homology of the coelom. A single pericardium formed by fusion in mollusks other than *Neopilina* is thus an apomorphy.

Molecular evidence

Recent sequencing of 18S ribosomal RNA among 22 classes (not including Aplacophora), in 10 animal phyla, split off acoelomate Platyhelminthes as sister group of the remaining bilaterian taxa, the eucoelomates, which fall into four closely rooted groups (Field *et al.*, 1988). The group termed Eutrochozoa (Ghiselin, 1988) includes five analyzed phyla: Mollusca, Annelida, Brachiopoda, Pogonophora, and Sipuncula. More recently Turbeville *et al.* (1992) have added Nemertini to the Eutrochozoa, basing their results on 18S rRNA and analyzing two Platyhelminthes, in addition to the single flatworm analyzed by Field *et al.* (1988). A re-analysis by Lake (1990) of the 1988 data positioned Sipuncula closest to Mollusca and Brachiopoda, with Annelida and Pogonophora as sister groups. The presence of hemerythrins in Brachiopoda, Sipuncula, and some Annelida affords independent support from molecular data for some of the results of Field *et al.* (Curry and Runnegar, 1990).

The relationships among Sipuncula, Mollusca, and Brachiopoda, however, remain unresolved, and possible synapomorphies of sipunculan and molluscan larval characters were not taken into account by Lake. Although the molecular evidence is still incomplete, it suggests that mollusks have descended from a coelomate ancestor, and that sipunculans are their closest sister group. In proposing that the last common ancestor of the Annelida-Mollusca lineage was hemocoelic and segmented, Lake did not discuss the presence or absence of a coelom. Ghiselin (1988) considered the evolution of Mollusca in light of the molecular evidence given in Field *et al.* (1988), amplifying the data with an analysis of specific nucleotides and a useful history of molluscan phylogenetic hypotheses. Ghiselin favored a segmented, coelomate eutrochozoan ancestor, with loss or reduction of segmentation in the Mollusca. Salvini-Plawen (1990), however, retained a preference for a turbellariomorph molluscan ancestry and refuted the validity of the sequencing by Field *et al.* (1988) and Ghiselin (1988), because "for some selected, traditionally monophyletic groups [including mollusks] euphemistic premises are made" by eliminating some data as convergences. Willmer and Holland (1991) also considered that mollusks had a flatworm origin and suggested that RNA analysis of several Platyhelminthes might show them to be poly- or paraphyletic, but the work of Turbeville *et al.* (1992) indicates that they are monophyletic.

Monophyly of Aplacophora

A proposed homology of the chaetoderm oral shield with the creeping sole of the archimollusk was the basis for separating the two aplacophoran taxa into two classes (Fig. 7B, C; Fig. 8A) (Salvini-Plawen, 1972, 1985, 1990). This homology was based on the innervation of the oral shield (Salvini-Plawen, 1972), the character of the epidermis, and the presumed homology of cuticular structures (Fig. 8C, arrowhead) (S. Hoffman, 1949), but it is not upheld either by light or transmission electron microscopy (Scheltema *et al.*, in press, fig. 9; Tscherkassky, 1989). The oral shield cuticle is continuous with that of the pharynx and is a lip, and the innervation of the shield is cerebral, lying anterior to that part of the anterior nervous system considered "tentacular," and thus part of the head region, by Ivanov (1991). Accordingly the two aplacophoran taxa cannot be separated on the basis of the chaetoderm oral shield, although Salvini-Plawen (1990) recently argued that the homology holds because the foregut and oral-shield epithelia are different, and the presence of the cuticle is secondary. In a schematic drawing through an oral shield, Salvini-Plawen (1990, fig. 7) showed a separation, the "mantle rim," between the oral shield cuticle and body cuticle, but this separation does not exist in my experience (Scheltema *et al.*, in press, fig. 9B). The argument would be clarified if it were known whether the oral shield is stomadeal in origin.

Several synapomorphies suggest that the two aplacophoran taxa are monophyletic. The outgroup for comparison is Polyplacophora.

The tetraneural nervous system, including the cerebral commissure, lateral and ventral nerve cords, and suprarectal commissure, is more heavily ganglionated in both neomenioids and chaetoderms than in chitons. The radula
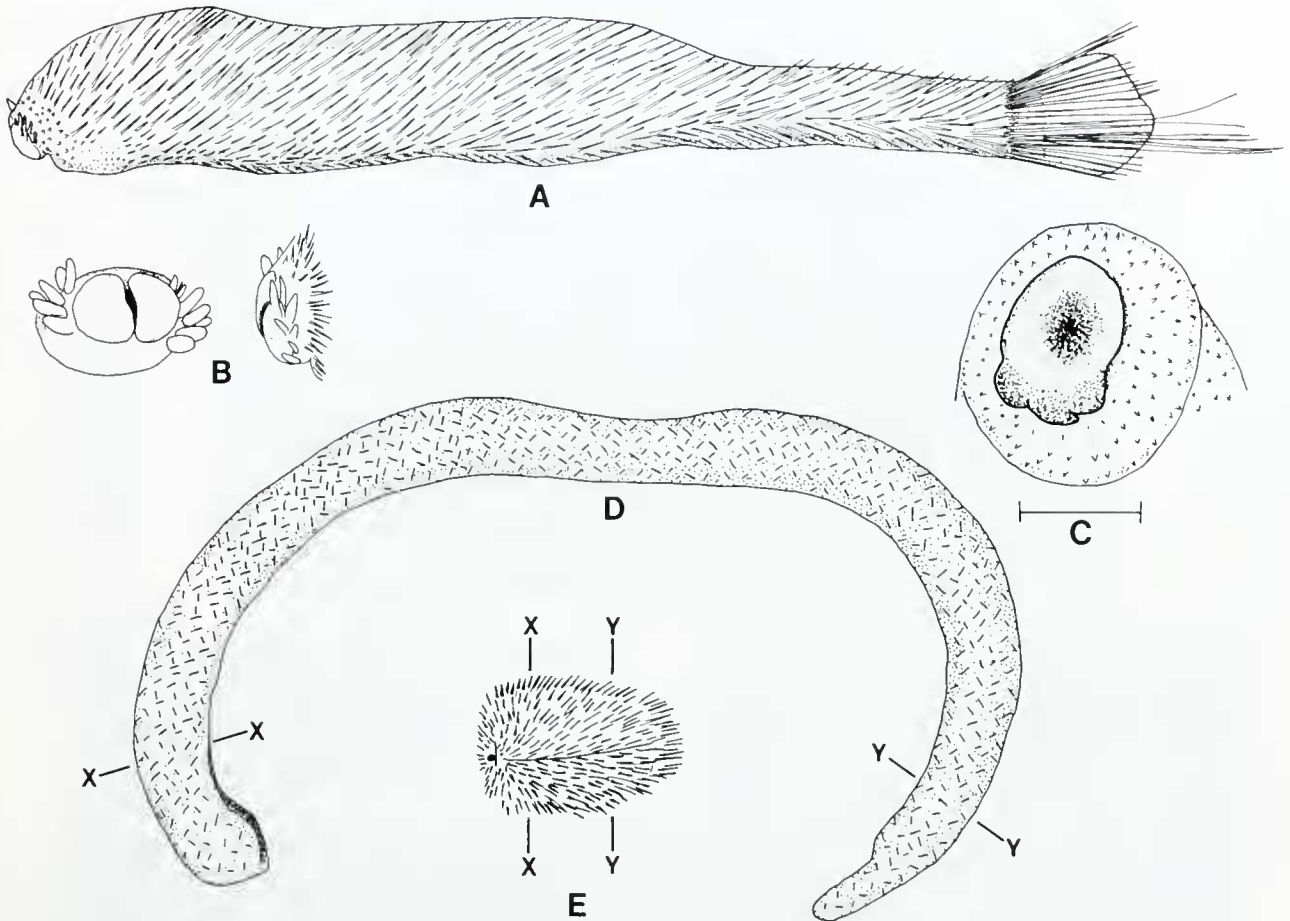
Figure 7. (A-C) Chaetodermomorpha. (A, B) *Chevroderma turnerae,* entire animal (anterior to left) and divided oral shield (from Scheltema, 1985, fig. 3L, O, P). (C) Oral shield of *Scutopus megaradulatus* (cf., Fig. 8A) (from Scheltema, 1988, fig. 6). (D, E) Neomeniomorpha. (D) *Dorymenia* sp. (E) A new neomenioid genus and species in the family Simrothiellidae. D and E are drawn to the same scale, anterior to left; the midgut and gonad lie between X-X and Y-Y.

in its plesiomorphic state in Aplacophora is distichous, that is, only two teeth per row (Scheltema, 1988; Scheltema *et al.,* 1989), a reduction in number from the docoglossate chiton radula. Both neomenioids and chaetoderms have a dorsoterminal sense organ (= dorsocaudal sensory pit), or sometimes several, in the epidermis. It is of unknown function, although homology to the osphradium has been conjectured (Spengel, 1881; Haszprunar, 1987). Whether or not this homology is correct, the position of the dorsoterminal sense organ is an autapomorphy of the Aplacophora, for there is no compelling evidence that this position, postulated to be primitive for the molluscan osphradium (Salvini-Plawen, 1985), is other than an apomorphy shared only by neomenioids and chaetoderms.

The two aplacophoran taxa share a similar reproductive system unique among mollusks. Paired gonads, sometimes fused, open directly into the pericardium, and paired U-shaped gametoducts lead from the posterior end of the pericardium, first anteriorly and then posteriorly, to the mantle cavity (Figs. 5A, 6A, 9D). Separate gonaduct openings in species of *Phyllomenia* (Salvini-Plawen, 1978) are interpreted here as a derived condition of that genus.

The mantle cavity in both neomenioids and chaetoderms is small and posterior, acting as little more than a cloaca. In neomenioids, the groove on either side of the foot-fold can also be considered as reduced mantle grooves (Figs. 6A, 8C). The paired ctenidia in chaetoderms, which fill most of the mantle cavity, is probably a plesiomorphy, with loss in the neomenioids resulting from the space requirements of a secondarily more complicated reproductive system, including sometimes very large copulatory spicules.

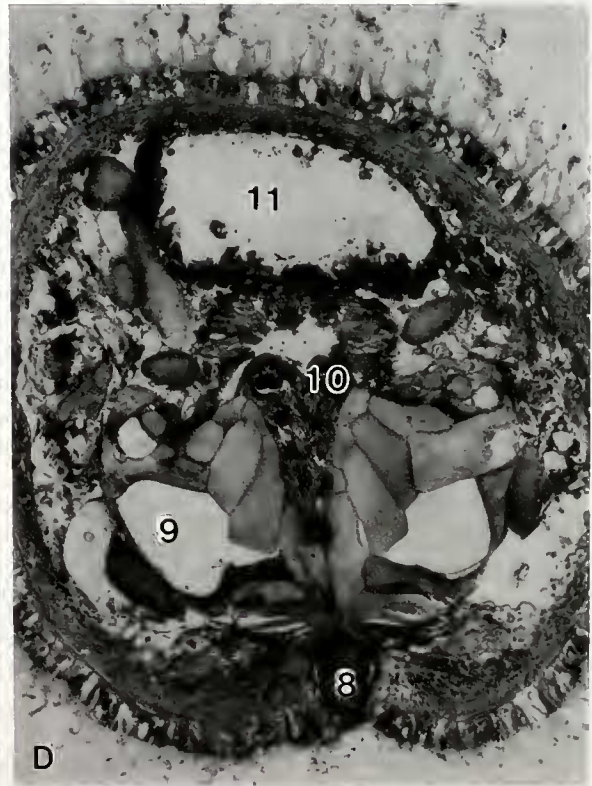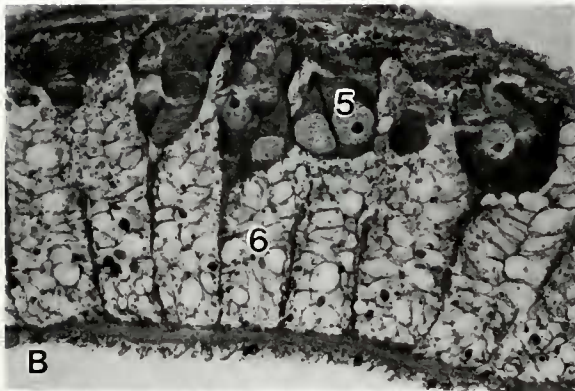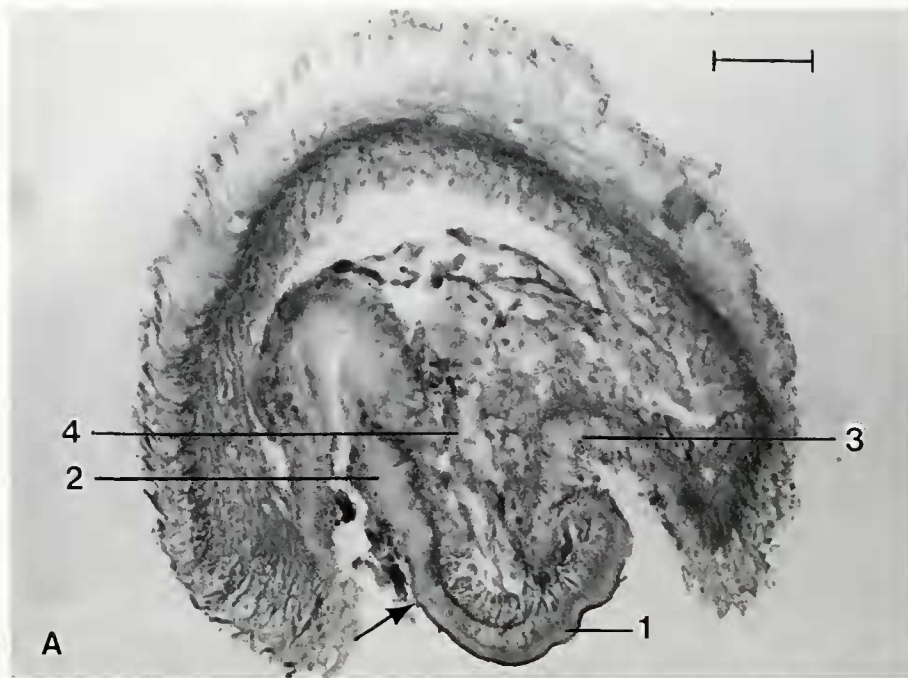Finally, the worm shape itself is here considered a synapomorphy of the Aplacophora, and not separate,

Figure 8. (A) Cross-section through the oral shield of a chaetoderm, *Scutopus megaradulatus,* showing continuity between pharyngeal and oral-shield cuticle. Arrow indicates transition between homogeneous pharyngeal cuticle and more specialized fibrillar oral-shield cuticle with a thickened outer layer (from Scheltema, 1988, fig. 5). (B) Sagittal section through a neomenioid, *Gymnomenia* sp., showing serial lateroventral musculature. (C) Cross-section through the nonmuscular, heavily ciliated foot of a neomenioid, *Helicoradomenia juani.* The arrowhead indicates the nonspiculose cuticle of the mantle cavity extending along each side of the foot groove, which was considered homologous to the chaetoderm oral shield by S. Hoffman (1949). (D) Cross-section through the radula, radula bolsters, and paired, hollow radula vesicles in *Helicoradomenia juani* (from Scheltema and Kuzirian, 1991, fig. 4D). 1 oral-shield cuticle, 2 pharyngeal cuticle, 3 cuticle of body wall, 4 nerve fibers from precerebral ganglion, 5 ovarian region of hermaphroditic gonad, 6 digestive cells of undifferentiated midgut, 7 copulatory spicule pocket, 8 foot, 9 radula vesicle, 10 radula, 11 dorsal cecum of stomach/digestive gland.
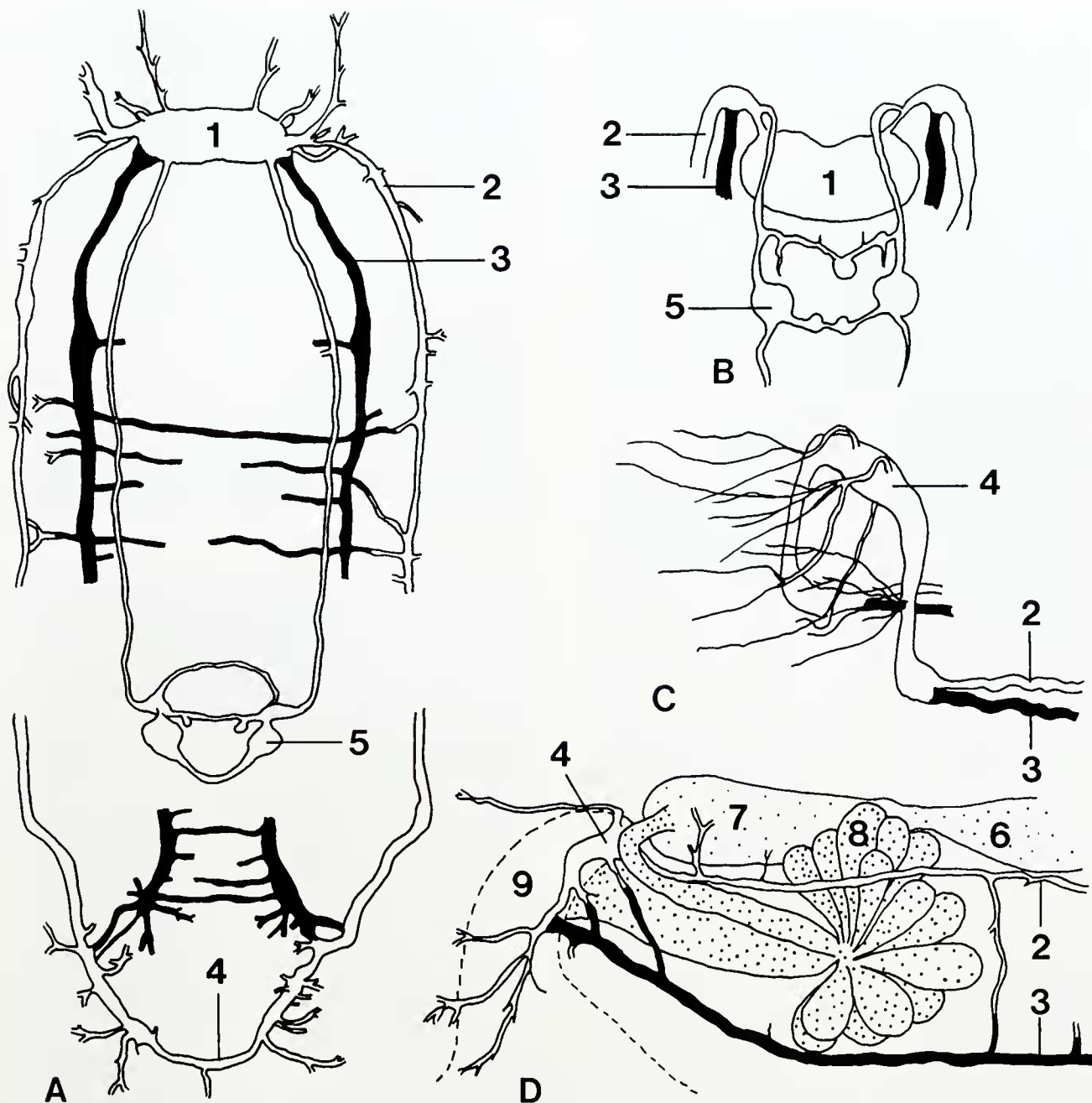
Figure 9. Nervous system and reproductive system in a neomenioid, *Strophomenia scandens* (A, D) and nervous system in a chaetoderm, *Limifossor talpoideus* (B, C). (A) Lateral (= pleural, visceral) cord with its origin in the cerebral ganglion separate from the origin of the ventral (= pedal) cord. Lateral and ventral cords remain separate posteriorly (after Heath, 1904, pl. 27, fig. 2). (B) Anterior end; the lateral and ventral cord have a single origin in the cerebral ganglion (after Heath, 1911, pl. 10, fig. 8). (C) Posterior end; the ventral cord runs close to the lateral cord and fuses with it. The suprarectal commissure is ganglionated (after Heath, 1905, pl. 43, fig. 18). (D) Posterior end; the lateral and ventral cords are well separated, with the separation maintained throughout. The gonad empties into the pericardium, which is shown in fine stippling. The U-shaped gametoduct, with a many-lobed seminal receptacle, is shown in coarse stippling; it runs from the posterior end of the pericardium to the mantle cavity, indicated by dashed lines (after Heath, 1904, pl. 27, fig. 6). 1 cerebral ganglion, 2 lateral cord, 3 pedal cord, 4 suprarectal ganglion/commissure, 5 buccal ganglion, 6 gonad, 7 pericardium, 8 seminal receptacle, 9 mantle cavity.

convergent apomorphies in the two taxa. When this character and those mentioned above are considered together, the Aplacophora clearly emerge as a monophyletic taxon.

Chaetodermomorpha, derived Aplacophorans

Neomeniomorpha are more similar than Chaetodermomorpha to the outgroup, the Polyplacophora, in nervous system (Fig. 9A, D), form of epidermal papillae (Fig. 6D, E), presence of anterior pedal glands (present only in the larvae of chitons) (Figs. 4, 6B), presence of paired pharyngeal glands, serial lateroventral musculature (Fig. 8B), and inequality of height and width dimensions. Several autapomorphies indicate that the burrowing Chaetodermomorpha have been derived from a creeping neomenioid-like ancestor. Criteria for considering a structure to be apomorphic are fusion or elaboration.

Changes in the nervous system are pronounced. In chaetoderms the lateral and ventral cord on each side have a single origin from the cerebral ganglion, whereas in nearly all neomenioids lateral and ventral cords have separate origins (Fig. 9A, B). In chaetoderms, the lateral and ventral cords on each side soon run close to each other, finally fusing into a single cord anterior to the suprarectal ganglion (Fig. 9C). In neomenioids, the cords remain apart and are well separated from each other (Fig. 9A, D). There are few commissures between the ventral cords in chaetoderms, and many in neomenioids. In chaetoderms, the suprarectal commissure and precerebral ganglia are larger and more swollen than in neomenioids.

Related to the loss of the ventral cord commissures, chaetoderms have entirely lost the foot and anterior pedal glands. The homology of mucous glands of the oral shield with pedal glands, proposed by S. Hoffman (1949), does not hold in TEM studies (Scheltema *et al.,* in press, Fig. 9A). In some species of *Scutopus* and *Psilodens,* ventral fusion of the mantle is marked by a longitudinal furrow between the spicules (Salvini-Plawen, 1968b; author's unpub. data).

The gut of chaetoderms is modified from the simple combined stomach-digestive gland midgut of neomenioids to a separate stomach and blind digestive gland. In its most derived state in Chaetodermatidae, there is a gastric shield and style sac with a mucoid rod (Scheltema, 1978; Salvini-Plawen, 1981b).

The serial lateroventral musculature of neomenioids (Fig. 8B) is lost in chaetoderms, although a few vestigial anterior bundles have been reported in a species of *Scutopus* (Salvini-Plawen, 1985). Body form in chaetoderms is circular in cross-section; in neomenioids there is usually a small but measurable difference between height and width. The circulatory system is somewhat better defined in chaetoderms than in neomenioids, with anterior and posterior vertical septa defining hemocoelic sinuses, and

with an often thick-walled aorta and aortal bulb (Scheltema, 1973) (Fig. 5A). Finally, the chaetoderm oral shield represents a specialized cuticular structure.

The autapomorphies of Chaetodermomorpha all seem to be related to their form of locomotion—burrowing in muds and silts—and feeding habits, either as carnivores on small benthic organisms, or as detritivores. Autapomorphies also exist in the Neomeniomorpha, particularly the sensory vestibule and rather complicated reproductive system with accompanying loss of mantle cavity ctenidia, but specializations of the Chaetodermomorpha mark them as the more derived of the two taxa.

Relationship of Aplacophora and Polyplacophora

Aplacophora and Polyplacophora are here considered to be sister taxa, the Aculifera, on the basis of shared characters of nervous system, spicules, and epidermal papillae. An attempt is made to determine the polarities of these characters, and other anatomical similarities are noted.

Nervous system

Aplacophora, Polyplacophora, and the monoplacophoran Tryblidiacea *Neopilina* and *Vema* all have a fully developed tetraneury, with paired lateral and pedal nerve cords arising from a cerebral commissure or ganglia and a circumoral or circumesophageal nerve ring. In the monoplacophorans, both cords are joined posteriorly ventral to the rectum, whereas in Aplacophora (Fig. 9) and Polyplacophora, only the lateral cords are joined, and they unite above the rectum in a commissure (chitons) or ganglion (aplacophorans). There is only a single cross-pedal commissure in the monoplacophorans and numerous ones in chitons and neomenioid aplacophorans.

What is the polarity of these two plans, both of which are plesiomorphic to more specialized nervous systems in other mollusks? Obvious outgroups for comparison, Annelida, Echiura, Nemertini, and Sipuncula, appear to have a reduced nervous system and offer no clues. In Annelida there is only a paired ventral cord, except for a secondarily derived tetraneury in Amphinomidae (Gustafson, 1930); in Nemertini there is a pair of lateral cords joined either above or below the rectum; in Echiura, there is a single ventral cord; and in sipunculans there is also a single ventral cord which is paired in the larval pelagosphera of *Phascolosoma agassizii* (Rice, 1973). One might surmise that *Neopilina,* a deep-sea deposit or xenophyophore feeder (Tendal, 1985), is less mobile than either aplacophorans or polyplacophorans and has retained a simpler nervous system, and the aplacophoran-polyplacophoran system is more specialized (derived) owing to habitat (chitons) or to carnivory (aplacophorans). Of course, a secondary loss and shifting of nerve elements in the monoplacophorans might also be considered, and Wingstrand

(1985) and Salvini-Plawen (1972) suggest that the sub-rectal commissure is an apomorphy. Whichever interpretation is correct, one can say that monoplacophoran and aplacophoran-polyplacophoran nervous systems are each apomorphic to some unknown ancestral state, and the suprarectal ganglion or commissure of the Aplacophora-Polyplacophora serves to relate them phylogenetically and set them apart from the Monoplacophora.

Spicule formation

Spicule formation in aplacophorans and polyplacophorans has most recently been investigated by Haas (1981) (Fig. 10). Spicules in both taxa are aragonite and formed extracellularly within an invagination of a single basal cell, which secretes calcium carbonate within a crystallization chamber sealed by neighboring cells (Scheltema *et al.*, in press, fig. 6D). In chitons, megaspines are formed from a proliferation of the basal cell and do not occur in aplacophorans.

Spicules of the Aculifera are usually considered to be a plesiomorphic state of calcium carbonate formation within Mollusca, since both spines and shell occur in chitons and only spines occur in Aplacophora, both being "primitive" groups in the general sense. However, Monoplacophora, likewise considered primitive, have no spines.

The dorsal, calcium-carbonate-secreting epidermis of Mollusca, in combination with a ventral locomotary surface, is probably an apomorphy. However, the shell-bearing Brachiopoda are rooted with the Mollusca-Annelida group by RNA sequencing (Field *et al.*, 1988), and some boring Sipuncula have calcium carbonate deposits at the dorsal anterior end of the trunk (Rice, 1969). Further comparative work needs to be done to compare calcium carbonate secretion among the Eutrochozoa before homology can be assumed.

It cannot be concluded from outgroup comparison that spicules and shell are homologous structures (and the argument will be made further on that they are not), or that either is the plesiomorphic state. It can be concluded, however, that because of the way in which they are formed, spicules of Aplacophora and Polyplacophora are homologous and can be construed as a synapomorphy.

Epidermal papillae

The epidermis of both chitons and aplacophorans are liberally supplied with secretory papillae (Fig. 6D, E). In chitons, papillae are homologous with aesthetes (Fischer *et al.*, 1980). Although homology with other conchiferan shell-penetrating structures has been suggested (Salvini-Plawen, 1985), the homology was considered spurious by Wingstrand, who reviewed the literature on the subject (1985, pp. 58–59). The presence of these papillae is con-
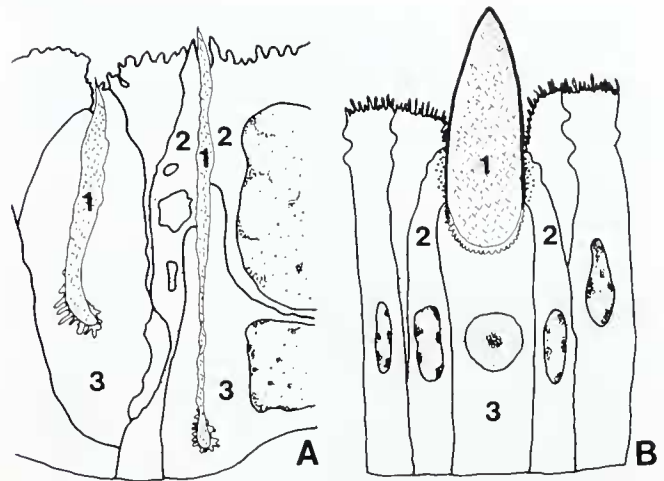

Figure 10. Spicule formation in (A) Aplacophora and (B) Polyplacophora (after Haas, 1981, figs. 6, 12). The spicule is formed within an invagination of a basal cell which secretes $CaCO_3$. The crystallization chamber is sealed by a ring of neighboring cells, which in Polyplacophora produce a pellicle around the spicule. 1 spicule, 2 neighboring cell, 3 $CaCO_3$-secreting basal cell.

sidered here to be an apomorphy of the Aplacophora-Polyplacophora.

Reduced serial replication

Compared to Monoplacophora, there is less serial replication in both Polyplacophora and Aplacophora, but both have greater serial replication than other mollusks. Serial replication appears as regular, lateroventral musculature in Neomeniomorpha (Fig. 8B) and as 8-fold repetition of muscles and shell plates in chitons.

Other anatomical homologies

Aplacophorans and polyplacophorans share certain other anatomical structures that are probably homologous, but they may be plesiomorphies of the Mollusca. Dorsal paired gonads, becoming fused during ontogeny in chitons and most Chaetodermomorpha, lie like sacs more or less free above the gut and digestive gland in the dorsal hemocoel. In *Neopilina*, the gonad is ventral to the digestive system (Lemche and Wingstrand, 1959), and in many other Mollusca the gonad is intermingled closely with lobes of the digestive gland. The circulatory system in both groups is extremely open with posterior paired auricles and a ventricle, a dorsal aorta leading to the head (lacking in many Neomeniomorpha), and open sinuses, the latter more profuse in chitons.

Taken together, the above reasons are sufficient for concluding that Aplacophora and Polyplacophora belong together in a single taxon, the Aculifera, which is therefore a clade, and not a grade.

Aculifera as the Sister Taxon of the Conchifera

Chitons provide evidence that Aculifera are separate from their sister group, the Conchifera. The evidence is based on shell ontogeny, shell structure, and perhaps molecular data.

Shell ontogeny

In Conchifera, the shell originates within an ectodermal invagination, the shell-field invagination, which is covered by an organic pellicle (Eyster and Morse, 1984) (Fig. 11). In *Aeolidia papillosa*, long cytoplasmic processes overlie the pellicle. In chitons, there is no shell field invagination, and shell plate anlagen are deposited within transverse depressions which are sealed, not by a pellicle, but by long, overlapping microvilli that lie beneath a gelatinous mucoid substance (Kniprath, 1980; Haas *et al.*, 1980; Haas, 1981; see Scheltema, 1988, for a more complete discussion). Furthermore, in healthy larvae, shell is not deposited as separate granules, as illustrated by Kowalevsky (1883), but as uninterrupted rods (Kniprath, 1980). This fact conflicts with the hypothesis that chiton shell arose from fused spicules (Salvini-Plawen, 1985, 1990).

Shell structure

The crystallography of chiton shell has been said to indicate an autapomorphy of chitons by Haas (1976), who found that "The . . . c-axis of [the] hypostracum lies in the bisectrix of the crystalline fibers. The whole complex acts crystallographically as a single crystal" (p. 392). If this crystallographic orientation is correct, then no homology exists between polyplacophoran and conchiferan shell. Further differences are a lack of true periostracum in chitons (although Haas [1981] has demonstrated a thin cuticle overlying the shell plates) and a lack of a nacreous layer (for further discussion see Wingstrand, 1985; and Scheltema, 1988). On the other hand, the shell of the tryblidiacean Monoplacophora does not differ from other primitive conchiferan shells (Lemche and Wingstrand, 1959).

Molecular evidence

The evolutionary tree of 18S rRNA has three branches for three classes of mollusks—a nudibranch, two species of clam, and a chiton. This trifurcation of mollusks also appears in Lake's (1990) re-analysis of the data. Further molecular data for all molluscan classes should resolve the branching, but there is a hint of molecular distance between chitons and the two other classes analyzed.

Evidence for Progenesis in Aplacophora

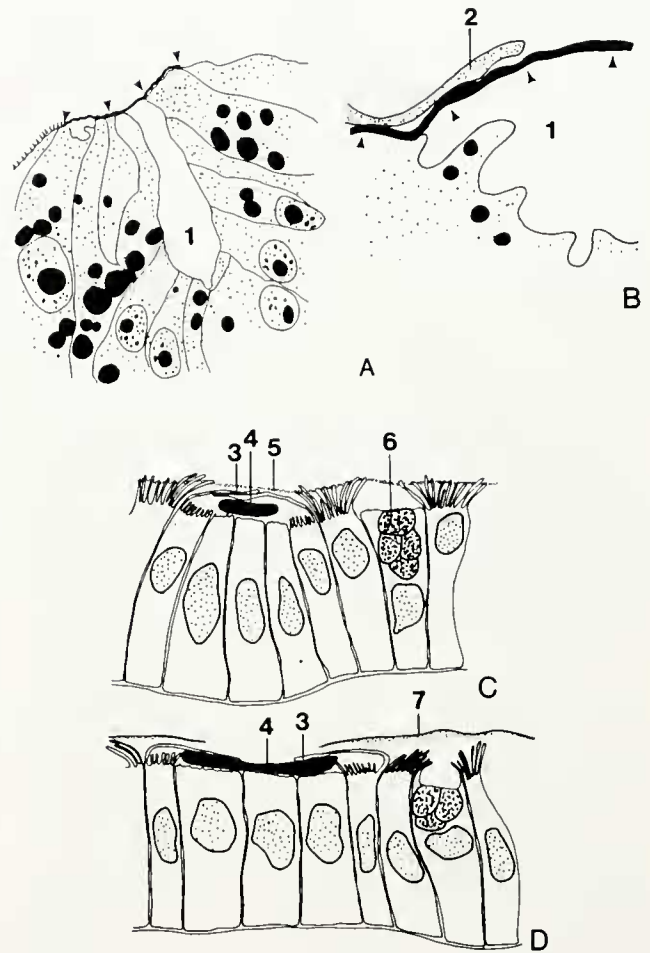A vermiform body is a character that could have been added rapidly by a small change in a regulatory gene or

Figure 11. Shell deposition in larvae of Conchifera and Aculifera. (A, B) Gastropod, *Aolidia papillosa.* An organic pellicle (arrowheads) covers the lumen of the shell field invagination; a cytoplasmic extension shown in B seals the edge of the pellicle (after Eyster and Morse, 1984, figs. 1, 2; from Scheltema, 1988, fig. 4). (C, D) Polyplacophoran, *Ischnochiton rissoi.* The shell plate is first secreted beneath microvilli (stragulum) which are covered by a layer of mucus (C); later (D) the microvillar processes have pulled apart and a cuticle begins to form (after Kniprath, 1980, fig. 5, from Scheltema, 1988, fig. 4). Haas (1981) illustrated a similar process except for showing that cuticle covered the stragulum before $CaCO_3$ deposition. 1 shell field invagination, 2 cytoplasmic extension, 3 microvillar process (stragulum), 4 calcium carbonate of shell plate, 5 mucous layer, 6 ?mucous cell, 7 cuticle.

in timing of cell assembly early in the ontogeny of an aculiferan mollusk (for mechanisms and examples see Raff and Kaufman, 1983; McKinney and McNamara, 1991). In the embryological development of the chiton *Lepidopleurus asellus*, swimming larvae are first oval and then become secondarily flattened and sink to the bottom (Christiansen, 1954). Even with development of the foot, chiton larvae remain ovoid for a time (Heath, 1899, Fig. 52; Eernisse, 1988, Fig. 7). One can imagine that larvae of some aculiferan, not necessarily a chiton, might not

have become dorsoventrally flattened through a small change in gene regulation and the worm-like shape arose.

The change to a vermiform shape could have occurred either early in the evolution of Mollusca or late. Recent phylogenies presume that a vermiform shape evolved as an early offshoot of the Mollusca, placing Aplacophora closest to the stem form, either as a monophyletic clade (Scheltema, 1988; Wingstrand, 1985), or as two separate clades, with the Chaetodermomorpha evolving first as the sister-group to all extant Mollusca (Salvini-Plawen, 1972, 1985). Serial replication thus was seen to be an apomorphy. If Aplacophora are closest to the molluscan ancestor, then the imperatives following from that phylogenetic construct fit poorly with the arguments given above, that is: (1) Aplacophora and Polyplacophora are a clade; (2) shell is not formed by fusion of spicules; and (3) chiton shell is not homologous to conchiferan shell. The question of when serial replication evolved in mollusks becomes critical, for it is either a plesiomorphy of mollusks, or not.

Polyplacophora, belonging to Aculifera, have some structures homologous with Monoplacophora, belonging to Conchifera, that are not shared with the Aplacophora (Wingstrand, 1985): radula dentition and radular apparatus including musculature; 8-serial pedal retractors; pre-oral unpaired fold, or velum; perhaps the heart with two pairs of atria; and coiled intestine. Wingstrand noted that some of these structures "could be plesiomorphic, *i.e.*, could have been present already in some Aplacophoran ancestors" (1985, p. 74), but considered that the radula and radular apparatus, in particular the paired, hollow radula vesicles, are synapomorphies. It was not then known that paired radular vesicles are also present in some neomenioids (Fig. 8D). Here, structures argued to be apomorphic by Wingstrand are considered plesiomorphic with exception of the coiled gut, a character widely convergent among mollusks. Thus, serial replication is here considered a plesiomorphy of Mollusca.

The possibility that a worm shape was acquired by aplacophorans late in aculiferan evolution leads to a wholly different concept of molluscan phylogeny. It calls for progenesis in Aplacophora, wherein nonserial but plesiomorphic-appearing anatomical characters are retained. The following evidence supports the hypothesis that Aplacophora are progenetic; *i.e.*, that they have retained ancestral juvenile characters in adult form through acceleration of sexual maturation (Gould, 1977).

(1) If narrowing of the body by acquisition of a worm shape arose early in aculiferan evolution without progenesis, then this process should be reflected somehow in the internal anatomy, and the more elongate (that is, narrower) the shape, the more pronounced should the internal changes become. Within the Neomeniomorpha, the least derived aplacophoran taxon, there is little organizational difference between short and elongate species in anterior and posterior ends or in musculature. Elongation of external form is accompanied internally by a simple lengthening of the gonad and midgut (Fig. 7D, E). The situation in the more derived chaetoderms differs and does not serve the argument.

A comparison can be made to *Cryptoplax*, a genus of chiton with a derived worm-like shape. In *Cryptoplax* there are at least four specializations of adult characters: (a) the mantle is very thick relative to internal body diameter; (b) there is loss of circulatory pathways; (c) there is loss of shell and shell musculature; and (d) the intestinal tract is remarkably long and complicated, turning back on itself in numerous spirals (Wettstein, 1904; H. Hoffmann, 1929-30). Furthermore, an analysis of the allometric equation defining shape in 408 chiton species in 39 genera indicated great uniformity in allometry, except in the carnivorous *Placiphorella* and in genera of Cryptoplacidae (Watters, 1991). Species of Cryptoplacidae, except those in the most primitive genus, are allometrically similar to each other but have shifted markedly from the allometry of other chitons. Although no allometric studies have been made of neomenioids, the extremes in vermiformity (Fig. 7D, E) do not predict uniformity. Thus there may be an ontogenetic difference in the evolutionary pathway to a worm-like shape taken by the two aculiferan taxa. Progenesis, an intrinsic process, is hypothesized for Aplacophora, and selection working on structural genes, an extrinsic process, for *Cryptoplax*.

(2) Progenesis results in early reproduction (Gould, 1977). One abundant northwestern Atlantic aplacophoran species living at 2000 m, *Prochaetoderma yongei*, is known to mature within one year, a remarkably rapid rate, given the ambient temperature ($\sim 3°C$) and in comparison with other cold-water mollusks. *P. yongei* is interpreted as being an opportunistic species (Scheltema, 1987), but since it is the only aplacophoran for which even part of the life history is known, one cannot be sure that early reproduction is the usual case in Aplacophora.

(3) Progenesis results in a reduced body size (Gould, 1977), but the size of the nearest ancestor to Aplacophora is, of course, unknown. Most neomenioids are usually less than 5 mm long, and one can only infer from the generally larger size of chitons that the first ancestral aplacophoran was already small. Like some other deep-sea taxa, such as protobranch bivalves (Sanders and Allen, 1973) and isopods (Hessler *et al.*, 1979), aplacophorans have evolved primarily in the deep sea, where they reach their greatest diversity (Scheltema, 1990). Food is limiting there, and small body size of macrobenthic organisms is the norm (Monniot and Monniot, 1978; Allen, 1983; Soetaert and Heip, 1989). Large neomenioids do exist in the deep sea, but they are usually either specialized (giant *Neomenia* species: Baba, 1975; Kaiser, 1976) or live in environments where there is high productivity (*e.g.*, high

latitudes: *Proneomenia sluiteri*, Derjugin, 1915, 1928). Large body size in Aplacophora is probably an apomorphic character because it is found scattered amongst unrelated families, some of which have derived characters such as loss of radula or a thick dermis.

(4) Certain structures in Aplacophora are less developed than homologous structures in Polyplacophora or other mollusks. (a) The organic composition of the cuticle is simpler than in chitons (Beedham and Trueman, 1968). (b) The radula in its plesiomorphic state in neomenioids has only two teeth per row (distichous), a condition found in the early ontogeny of several gastropods (Kerth, 1983; Scheltema, 1988; Scheltema *et al.*, 1989). (c) The aplacophoran mantle cavity, located ventroposterior to posterior, is small, serving as little more than a cloaca (Fig. 7A, D). (d) Both neomenioids and chaetoderms lack kidneys. (e) The foot is developed only as a ciliated ridge without musculature in neomenioids (Fig. 6A). (f) Gonads and pericardium are united in aplacophorans, reflecting the early ontogenic state in chitons, where the gonad originates as an anlage of the pericardium (Hammarsten and Runnström, 1925) (Figs. 5A, 6A, 9D). (g) The gut in neomenioids is simple, with a united stomach and digestive gland; the digestive gland is separate from the stomach in other mollusks.

(5) Aplacophora have retained a structure found in chitons only as larvae. The anterior pedal glands are large and specialized in neomenioids (Fig. 6B, C), but are lost soon after metamorphosis in chitons, where they serve only for early postmetamorphic attachment (Heath, 1899) (Fig. 4B).

Although progenesis results in primitive-appearing structures, they are actually derived. Therefore, some process within the Aculifera should be primitive in the Polyplacophora but derived in the progenetic Aplacophora. Such seems to be the case in early embryological development. Freeman and Lundelius (1992) have proposed that, among the spiralian coelomates Mollusca, Annelida, Sipuncula and Echiura, two mechanisms determine which blastomere is specified as the D quadrant. They hypothesized that the primitive mechanism for D quadrant specification is by induction after the fifth cleavage, when one of the four macromeres has maximum contact with the micromeres. The derived mechanism is by segregation of the cytoplasm into one macromere, which is then specified as the D quadrant; it occurs by the second cleavage. In Polyplacophora, macromeres cleave equally and the D quadrant is specified by induction, the primitive mechanism. But in the cleaving egg of the neomenioid *Epimenia*, a polar body is formed and therefore macromeres of unequal size; thus the D quadrant is specified by cytoplasmic determinants, the derived mechanism (Baba, 1951; Freeman and Lundelius, 1992).

The evidence for progenesis presented here argues for heterochrony in the Aplacophora, but this idea cannot be tested either against fossils, which are unknown, or against a more complete phyletic lineage, as has been done for progenetic meiofaunal forms (Westheide, 1987) and deep-sea tunicates (Monniot and Monniot, 1978). When the early embryological development of aplacophorans is better known, and with further intrataxon comparative studies, the validity of the hypothesis may be clarified.

Phylogeny of the Mollusca

The phylogeny represented in Figure 12 proposes: a coelomate molluscan ancestor with serial replication; two separate evolutionary molluscan lineages, the Conchifera and the Aculifera, based on synapomorphies of differences in $CaCO_3$ deposits; and morphologies arising from progenesis in the Aplacophora.

The molluscan ancestor is considered to have had the following plesiomorphies: (1) extracellular $CaCO_3$ deposition by the dorsal epidermis (Mollusca generally); (2) serial replication, probably originally 8-fold (Monoplacophora, Polyplacophora, *Nautilus*, neomenioids, some bivalves); (3) coelom from the 4d cell, paired pericardial cavities (in Monoplacophora, and fused but large in Aplacophora and Polyplacophora); (4) radula, radular apparatus with hollow radula vesicles (Polyplacophora, Monoplacophora, Aplacophora, Fig. 8D); (5) nervous system poorly ganglionated, with cerebral ganglia and commissure, circumenteric ring, and paired lateral and pedal cords with cross-commissures and posterior connection (Monoplacophora in part, Aplacophora and Polyplacophora); (6) dorsoventrally flattened, small size (Cambrian Mollusca: Runnegar and Pojeta, 1985; Haszprunar, 1992; but note that the Cambrian fossil halkierids and *Wiwaxia*, perhaps near relatives of mollusks, are centimeters in length [Conway Morris, 1985; Conway Morris and Peel, 1990]); (7) dorsal cuticle (Aplacophora, Polyplacophora); (8) ventral ciliated locomotory sole (Mollusca generally); (9) head separate from the locomotory sole and with cerebral ganglia (Mollusca generally); (10) a groove between the dorsal and ventral surfaces, the future mantle cavity (Mollusca generally); (11) pre-oral fold; (12) the presence of podocytes in pericardial tissue (mollusks generally); (13) ductless anterior pedal mucous glands (as a glandular epithelium in Monoplacophora; Lemche and Wingstrand, 1959); (14) a one-way gut with mouth, anus, large digestive gland poorly differentiated from stomach (Neomeniomorpha, Monoplacophora); (15) paired pharyngeal diverticula; (16) poorly defined circulatory system; and (17) gonad and pericardium joined at least during ontogeny (Mollusca generally).

The phylogeny presented in Figure 12 requires that the original calcium carbonate deposition in mollusks was
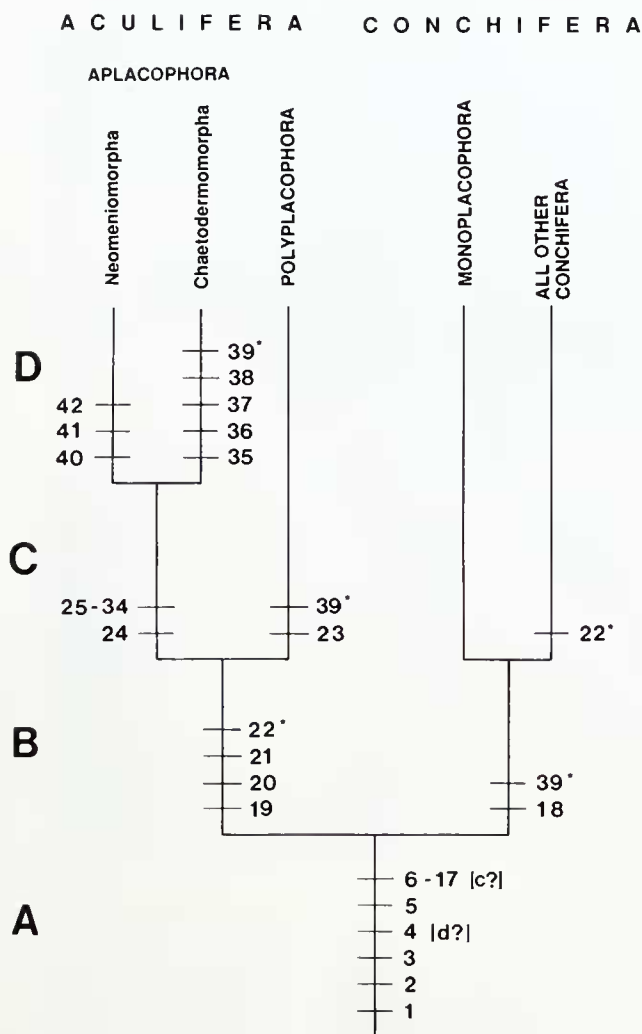
ACULIFERA   **CONCHIFERA**

APLACOPHORA

Neomeniomorpha · Chaetodermomorpha · POLYPLACOPHORA · MONOPLACOPHORA · ALL OTHER CONCHIFERA

D
39*
38
42 · 37
41 · 36
40 · 35

C
25-34 · 39*
24 · 23 · 22*

B
22*
21
20 · 39*
19 · 18

A
6-17 |c?|
5
4 |d?|
3
2
1

Figure 12. Proposed phylogeny of extant "primitive" Mollusca. (A) Apomorphies of Mollusca: 1 extracellular CaCO₃ deposition by dorsal epidermis; 2 eight-fold serial replication; 3 paired coelom, including pericardium; 4 radula; 5 poorly ganglionated tetraneury; 6 small size, dorsoventrally flattened; 7 dorsal cuticle; 8 ventral locomotory sole; 9 head separate from sole; 10 groove between dorsal and ventral surfaces; 11 pre-oral fold; 12 nonsegmented pericardium, pericardial tissue with podocytes; 13 ductless anterior pedal gland; 14 poorly differentiated stomach/digestive gland (model: *Neopilina*); 15 paired pharyngeal diverticula; 16 poorly defined circulatory system; 17 joined gonad/pericardium during early ontogeny. (B) Separation of Conchifera and Aculifera: 18 calcareous shell; 19 spicules; 20 epidermal papillae; 21 suprarectal ganglion/commissure; 22 reduced serial replication and fused pericardium. (C) Separation of Polyplacophora and Aplacophora (24–31 the result of progenesis): 23 eight shell plates; 24 worm shape; 25 reduced foot; 26 reduced mantle cavity; 27 joined gonad/pericardium; 28 kidneys absent; 29 chemically simple cuticle; 30 serial lateroventral musculature; 31 distichous radula; 32 U-shaped gametoducts; 33 ganglionated nervous system; 34 dorsoterminal sense organ. (D) Separation of Chaetodermomorpha and Neomeniomorpha: 35 ventrally fused cuticle, foot lacking; 36 oral shield; 37 fused, reduced nervous system; 38 serial replication absent; 39 stomach separate from digestive gland; 40 large anterior pedal gland; 41 elaborated reproductive system; 42 ctenidia absent. * = convergent morphologies; c? = presence of ctenidia questionable; d? = radula questionably docoglossate.

neither as spicules nor as shell. CaCO₃ was first deposited, perhaps, as granules within a dorsal cuticle, which was thereby stiffened. Such a reinforced cuticle could act as the antagonist to the dorsoventral pedal musculature. During chiton ontogeny, the pedal musculature develops earlier than the shell plates (Hammarsten and Runnström, 1925). One can speculate from this fact that, perhaps, the various forms of shell and spicules among mollusks have resulted from selection for different modes of locomotion in various habitats, rather than selection just for protection.

In terms of CaCO₃ secretion among phyla, the important synapomorphy for mollusks, which sets them off from other spiralian coelomates, is the locomotary sole in combination with a cuticle- and CaCO₃-secreting dorsal epidermis. Certain rock-boring sipunculans also secrete CaCO₃ dorsally, forming a plug for their tubes (Rice, 1969), and Brachiopoda, which fall in with spiralian coelomates in molecular analysis, also have calcium carbonate shells. However, animals in neither of these phyla have the combination of dorsally produced CaCO₃ and a ventral locomotary surface unique to mollusks.

It is hypothesized that after, or as, Conchifera diverged from the stem line, the mantle deepened and gills developed. Serial replication was retained in Monoplacophora but lost in the rest of the Conchifera, except for serial pedal musculature in some taxa and the renal system in cephalopods. Aculifera may have evolved either at the same time as Conchifera or later. By the Upper Cambrian or Lower Ordovician, the serial shell plates of Polyplacophora had evolved (Runnegar and Pojeta, 1985). This event was preceded by the loss of serial replication other than lateroventral muscles and perhaps by an increase in size. In a separate evolutionary event of progenesis, the Aplacophora evolved with probable reduction in size, further loss of serial replication, loss of nephridia, retention of gonad-pericardial connection, and acquisition of a worm shape with concomitant reduction of the foot. Chaetodermomorpha were derived from the neomenioid-like stem with complete loss of foot, reduction and fusion of the nervous system, and specializations of the gut.

This hypothesized phylogeny does not call for an evolutionary process in which CaCO₃ deposits, or the cells that produce them, become fused. Furthermore, it should allow some of the Early Cambrian sclerite-bearing forms now coming to light, such as the shell-bearing, articulated halkieriid described recently from the Lower Cambrian of Greenland (Conway Morris and Peel, 1990), to find their place in relation to the extant Mollusca.

In this phylogeny, the Monoplacophora with clear serial replication are not evolved after Aplacophora, and molluscan serial replication is considered to be a plesiomorphy. As Wingstrand (1985) pointed out, it is difficult to imagine that serial replication evolved after the shell. The

careful and original anatomical analysis of Wingstrand showing close affinities of the monoplacophoran Tryblidiacea and Polyplacophora are upheld here as retained plesiomorphics of the common ancestor. Whether Pruvot's neomenioid larva with its supposed seven rows of spicules actually exists does not change the argument (see Salvini-Plawen, 1972, 1981a, 1985; Scheltema, 1988 for discussions and figures of the larva). Manuscript drawings of *Chaetoderma nitidulum* larvae made by G. Gustafson show eight rows of spicules for this taxon as well. If further observations on aplacophoran development prove that serial rows of spicules do exist, the larva still would not necessarily reflect progressive evolution from spicules to fused shell plate formation, but more likely would indicate a breakdown of plate formation similar to the breakdown of larval chiton shell plates caused experimentally by Kniprath (1980) (See also Scheltema, 1988).

Age of the Aplacophora

If known fossils reflect the actual time of evolutionary events, then the evolution of Polyplacophora late in the Cambrian (Runnegar and Pojeta, 1985) from a continuing line of aculiferous creatures was probable, with increased size and muscles being the determinants of shell plates rather than vice versa (see Hammarsten and Runnström, 1925, p. 276, for ontogenetic development of muscle before shell). Aplacophora, with their highly derived shape and paedomorphic internal organization, give information about the primitive conditions of mollusks without being themselves primitive. A Late Cambrian-Early Ordovician origin from an aculiferan form with a developed mantle groove and posterior mantle cavity is postulated for Aplacophora, with the 8-fold dorsoventral muscles rearranged in neomenioids into a series of indeterminate number.

Cautionary Notes on Convergences

Digestive system

The molluscan gut appears to have evolved similar morphologies more than once (Fig. 12, no. 39). Evidence for convergence lies in presence of the style sac and gastric shield, found in a number of molluscan classes. In the aplacophoran family Chaetodermatidae, one of the most derived of the chaetoderm groups based on radula morphology (Scheltema, 1972, 1981), the gut is the most complicated among chaetoderms, with a gastric shield and a mucoid rod in a style sac (Scheltema, 1978; Salvini-Plawen, 1981b). The polarity of a less to a more complicated gut configuration within the chaetoderms is clear (Scheltema, 1981). Thus, the presence of a style sac and gastric shield is convergent among Mollusca.

Metamerism

Reduction of serial replication (Fig. 12, no. 22) is hypothesized for several molluscan classes—Cephalopoda,

Bivalvia, Polyplacophora, and Aplacophora. The evidence from morphology, ontogeny, and molecular analysis seems not to favor the hypothesis that replication originated in annelids. If the altogether unsegmented Sipuncula are sister taxon of the mollusks, then arguments that the molluscan coelom is the result of a reduced annelid-like segmented coelom are not convincing.

Evidence presented here could be interpreted in three ways (Fig. 13, s^1–s^4). (1) A nonsegmented ancestor that had serial replication of organs and a coelom lies at the base of the lineage giving rise to Eutrochozoa (s^1). (2) The eutrochozoan ancestor had no serial replication, which
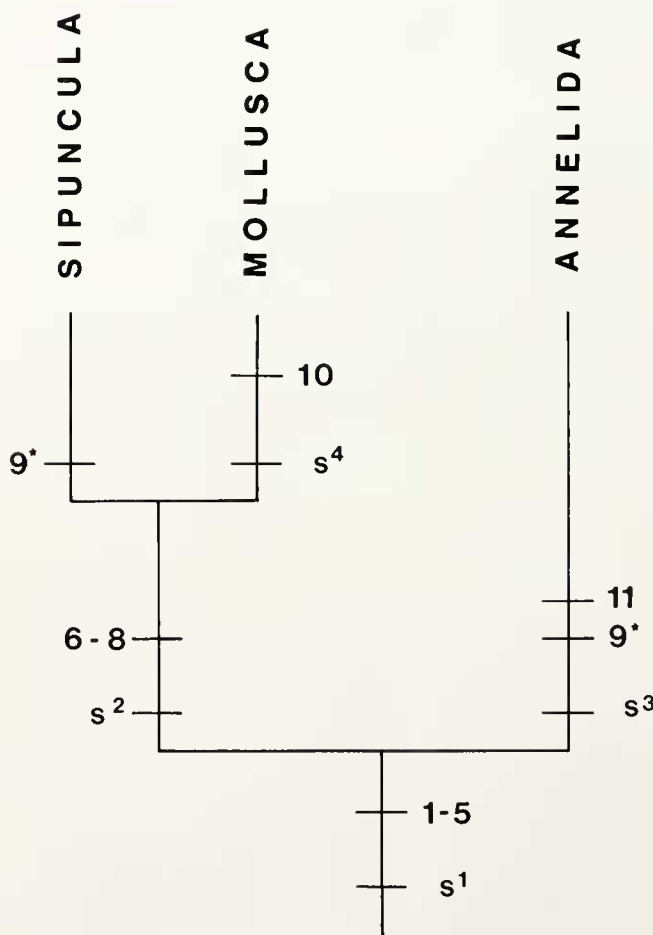

Figure 13. Phylogenetic relationship among Sipuncula, Mollusca, and Annelida. 1 spiral cleavage; 2 paired coelom originating from two teloblasts derived from 4d; 3 trochophore larva (?); 4 tetraneury; 5 ciliated creeping sole; 6 molluscan cross; 7 ventral, cuticular, pharyngeal (stomadeal), protrusible invagination and attendant musculature; 8 anterior pedal gland; 9 fused nerve cords; 10 reduced coelom; 11 loss of creeping sole. s = serial replication: s^1 symplesiomorphic for all three taxa, but lost in Sipuncula; s^2 symplesiomorphic for Sipuncula and Mollusca, but lost in Sipuncula, and convergent with s^3 as metamerism in annelids; s^3 metamerism plesiomorphic for Annelida, convergent with either s^2 or s^4; s^4 plesiomorphic for Mollusca, convergent with s^3. * = convergent morphologies.

later arose de novo twice: once in the stem form leading to mollusks and sipunculans (s^2), which was lost in the latter, and secondly in the ancestral annelid as metamerism (s^3). (3) Molluscan 8-fold serial replication (s^4) evolved after the stem form that gave rise to Sipuncula and Mollusca; and annelidan metamery (s^3) [as in (2)], arose as an unrelated evolutionary event. The first interpretation is perhaps closest to what may actually have occurred and seems the most parsimonious explanation.

Differences in the coelom among eutrochozoan groups can be related to locomotion, a theme emphasized—correctly, I believe—by Salvini-Plawen (*e.g.*, 1972, 1985). Locomotion among Eutrochozoa is most rapid in annelids and mollusks. Serial pedal musculature is related to a creeping locomotion and is the most conservative serial structure in mollusks, present as a plesiomorphy in Monoplacophora, Polyplacophora, Aplacophora, and (much reduced) Pelecypoda and perhaps the neritid Gastropoda. In Annelida, coelom and muscle have combined in the perfection of a hydraulic locomotion (Clark, 1964). Perhaps, then, a re-examination of the relationship of muscles and coelom during ontogeny would be a useful exercise in providing insights into understanding the development of metamerism in Eutrochozoa. For instance, in at least some Annelida, ectodermal segmentation of the three anterior segments precedes segmentation of mesoderm (Anderson, 1973, pp. 36–37).

Radula

Wingstrand (1985) gave a detailed description of the radular apparatus in Polyplacophora and Monoplacophora, demonstrating their great similarity, especially the docoglossate radula and radula vesicles. There are three possibilities: such a radula is a molluscan plesiomorphy; it is an apomorphy of Polyplacophora and Monoplacophora; or it is convergent.

Evidence from Aplacophora and ontogeny of some Gastropoda suggests that the plesiomorphic radula in mollusks was distichous (Kerth, 1983; Scheltema *et al.*, 1989). An outgroup for comparison is the Cambrian sclerite-bearing *Wiwaxia* (Conway Morris, 1985) with two or three rows of teeth which appear much like the plesiomorphic radula in Aplacophora. The phylogenetic position of *Wiwaxia*, however, remains enigmatic, considered either to be close to mollusks (Conway Morris, 1985) or to be an annelid (Butterfield, 1990). If the plesiomorphic radula is distichous, then the docoglossate radula is convergent in Polyplacophora, Monoplacophora, and patellacean Gastropoda. If the docoglossate radula is a molluscan plesiomorphy, it is difficult to imagine how it functioned in a small Cambrian mollusk and what evolutionary steps would be necessary to account for all other molluscan radulae.

The strongest evidence given by Wingstrand (1985) for monophyly of polyplacophorans and conchiferans is presence of a pair of hollow, presumably liquid-filled radula vesicles found at that time only in Polyplacophora and Monoplacophora. None had been reported in Aplacophora. However, a re-examination of the neomenioid *Helicoradomenia juani* and other species in the genus, which have a plesiomorphic aplacophoran radula, has led me to conjecture that paired, elongate, hollow vesicles present in this genus are a homolog to the radula vesicles in Polyplacophora and Monoplacophora (Fig. 8D). Therefore these vesicles are a molluscan plesiomorphy. However, further study of the aplacophoran radula and its apparatus is needed.

Larval forms

The phylogenetic significance of larval forms in Spiralia is not addressed here. There is still no agreement on whether a pelagic organism gave rise to benthic forms (*e.g.*, Nielsen and Nørrevang, 1985), or vice versa, and whether the trochophore larva arose once or several times (Ivanova-Kazas, 1985a, b, for careful discussions). Within Mollusca, Salvini-Plawen (1972, 1985) regarded the pericalymma larva, which lacks purely larval organs except the swimming test and is found only in aplacophorans and protobranch bivalves, as the ancestral type. The questions are left here as unresolved and not affecting the arguments for homology of early cell fate among Eutrochozoa, although my preference is indicated by use of the latter term.

Classification of Extant Molluscan Classes

With shell and spicules considered as synapomorphies for Conchifera and Aculifera, respectively, the following classification of extant Mollusca emerges:

Phylum Mollusca
  Subphylum Conchifera
    Class Monoplacophora
    Class Bivalvia
    Class Gastropoda
    Class Scaphopoda
    Class Cephalopoda
  Subphylum Aculifera
    Class Polyplacophora
    Class Aplacophora
      Subclass Neomeniomorpha
      Subclass Chaetodermomorpha

This arrangement is similar to that already proposed in the last century with little knowledge of the soft anatomy of Monoplacophora. Garstang (1896) considered the

Aplacophora as "degraded" from an ancestral chiton-like form, but although he later stressed the importance of paedomorphosis in evolution, he did not see it as pertaining to Aplacophora. It is curious that a classification based on what are here inferred to be synapomorphies and on progenesis should be much the same as classifications of a hundred years ago.

Conclusions

The hypotheses, arguments, and pieces of evidence presented here lead to the conclusions that Mollusca (1) are eucolomates with an ancestry in common with spiralian trochozoans; (2) are related to Annelida, but not as closely as they are to Sipuncula; (3) have a reduced coelom which was never segmented; (4) are not directly descended from an aplacophoran-like or turbellariomorph predecessor; and (5) are descended from an ancestor with serial replication.

Acknowledgments

Note added in proof: Two papers have just been published that have direct bearing on the ideas presented here. (1) Bengston S. 1992. The cap-shaped Cambrian fossil *Maikhanella* and the relationship between coeloscleritophorants and molluscs. *Lethaia* **25**: 401–420. *Maikhanella* is a genus of Lower Cambrian halkieriids with a cap-shaped shell formed of rows of embedded spicules, which were added by marginal accretion. Bengston discusses the possible homology with spicules of extant mollusks and with polyplacophoran shells. (2) Eernissee, D. J., J. S. Albert, and F. E. Anderson. 1992. Annelida and Anthropoda are not sister taxa: a phylogenetic analysis of spiralian and metazoan morphology. *Syst. Biol.* **41**: 331–344. Analysis by maximum parsimony among 141 morphological and embryological characters supports the concept of Eutrochoza, including the Mollusca.

Literature Cited

Allen, J. A. 1983. The ecology of deep-sea molluscs. Pp. 29–75 in *The Mollusca Vol. 6. Ecology,* W. D. Russell-Hunter, ed. Academic Press, Orlando, FL.

Anderson, D. T. 1973. *Embryology and Phylogeny in Annelids and Arthropods.* Pergamon Press, Oxford and New York. xiv + 495 pp.

Andrews, E. B. 1988. Excretory systems of molluscs. Pp. 381–448 in *The Mollusca, Vol. 11. Form and Function,* E. R. Trueman and M. R. Clarke, eds. Academic Press, San Diego, CA.

Baba, K. 1938. The later development of a Solenogastre, *Epimenia verrucosa* (Nierstrasz). *J. Dept. Agric. Kyusyu Imp. Univ.* **6**: 21–40.

Baba, K. 1951. General sketch of the development in a Solenogastre, *Epimenia verrucosa* (Nierstrasz). *Misc. Repts. Res. Inst. Nat. Res.* **19–21**: 38–46. [In Japanese with English summary.]

Baba, K. 1975. *Neomenia yamamotoi* spec. nov., a gigantic Solenogaster (Mollusca: Class Solenogastres, Family Neomeniidae), occurring in the north-eastern part of Japan. *Publ. Seto Mar. Biol. Lab.* **22**(5): 277–284.

Banta, W. C., and M. E. Rice. 1976. A restudy of the Middle Cambrian Burgess Shale fossil worm, *Ottoia prolifica.* Pp. 79–90 in *Proceedings of the International Symposium on the Biology of the Sipuncula and Echiura,* M. E. Rice and M. Todorović, eds. Institute for Biological Research "Siniš Stanković," Belgrade, and Smithsonian Institution, Washington, DC.

Beedham, G. E., and E. R. Trueman. 1968. The cuticle of the Aplacophora and its evolutionary significance in the Mollusca. *J. Zool.* **154**: 443–451.

Butterfield, N. J. 1990. A reassessment of the enigmatic Burgess Shale fossil *Wiwaxia corrugata* (Matthew) and its relationship to the polychaete *Canadia spinosa* Walcott. *Paleobiology* **16**: 287–303.

Christiansen, M. E. 1954. The life-history of *Lepidopleurus asellus* (Spengler) (Placophora). *Nytt Mag. Zool.* **2**: 52–72.

Clark, R. B. 1964. *Dynamics in Metazoan Evolution: The Origin of the Coelom and Segments.* Clarendon Press, Oxford. 313 pp.

Conway Morris, S. 1985. The Middle Cambrian metazoan *Wiwaxia corrugata* (Matthew) from the Burgess Shale and *Ogygopsis* Shale, British Columbia, Canada. *Phil. Trans. Roy. Soc. London, B* **307**: 507–586.

Conway Morris, S., and J. S. Peel. 1990. Articulated halkieriids from the Lower Cambrian of north Greenland. *Nature* **345**: 802–805.

Curry, G. B., and B. Runnegar. 1990. Partial amino acid sequences of hemerythrins from *Lingula* and a priapulid worm, and the evolution of oxygen transport in early metazoans. No. 4314, *Geol. Soc. Am. Abstr.* Dallas, TX.

Derjugin, K. M. 1915. [Fauna of the Kola gulf and its life conditions.]. *Mém. Acad. Imp. Sci. Petrograd* (ser. 8) 34(1): 1–929, t. 1–14 [Pp. 499–501 Solenogastres]. [In Russian]

Derjugin, K. M. 1928. Fauna des Weissen Meeres und ihre Existenzbedingungen. *Exp. Mers U.R.S.S.* fasc. 7–8, 1–511 [Pp. 294–295, Solenogastres].

Eernisse, D. J. 1988. Reproductive patterns in six species of *Lepidochitona* (Mollusca: Polyplacophora) from the Pacific Coast of North America. *Biol. Bull.* 174: 287–302.

Eyster, L. S., and M. P. Morse. 1984. Early shell formation during molluscan embryogenesis, with new studies on the surf clam, *Spisula solidissima Am. Zool.* 24: 871–882.

Field, K. G., G. J. Olsen, D. J. Lane, S. J. Giovannoni, M. T. Ghiselin, E. C. Raff, N. R. Pace, and R. A. Raff. 1988. Molecular phylogeny of the animal kingdom. *Science* 239: 748–753.

Fischer, F. P., W. Maile, and M. Renner. 1980. Die Mantelpapillen und Stacheln von *Acanthochiton fascicularis* L. (Mollusca, Polyplacophora). *Zoomorphologie* 94: 121–131.

Freeman, G., and J. W. Lundelius. 1992. Evolutionary implications of the mode of D quadrant specification in coelomates with spiral cleavage. *J. Evol. Biol.* 5: 205–247.

Garstang, W. 1896. On the aplacophorous Amphineura of the British Seas. *Proc. Malacol. Soc. London* 2: 123–125.

Gerould, J. H. 1906. The development of *Phascolosoma* Studies on the embryology of the Sipunculidae I. *Zool. Jahrb., Anat.* 23: 77–162.

Ghiselin, M. T. 1988. The origin of molluscs in the light of molecular evidence. Pp. 66–95 in *Oxford Surveys in Evolutionary Biology Vol 5*, P. H. Harvey and L. Partridge, eds. Oxford University Press, Oxford.

Gould, S. J. 1977. *Ontogeny and Phylogeny.* Harvard University Press, Cambridge, MA, and London.

Gustafson, G. 1930. Anatomische Studien über die Polychäten-familien Amphinomidae und Euphrosynidae. *Zool. Bidr. Uppsala* 12: 305–471.

Haas, W. 1976. Observations of the shell and mantle of the Placophora. Pp. 389–402 in *The Mechanisms of Mineralization in Invertebrates and Plants*, N. Watabe and K. M. Wilbur, eds. Belle W. Baruch Library in Marine Science 5.

Haas, W. 1981. Evolution of calcareous hardparts in primitive molluscs. *Malacologia* 21: 403–418.

Haas, W., K. Kriesten, and N. Watabe. 1980. Preliminary note on the calcification of the shell plates in chiton larvae (Placophora). Pp. 67–72 in *The Mechanisms of Biomineralization in Animals and Plants*, M. Omori and N. Watabe, eds. Tokai University Press, Tokyo.

Hammarsten, O. D., and J. Runnström. 1925. Zur Embryologie von *Acanthochiton discrepans* Brown. *Zool. Jahrb. Anat.* 47: 261–318.

Haszprunar, G. 1987. The fine morphology of the osphradial sense organs of the Mollusca. IV. Caudofoveata and Solenogastres. *Phil. Trans. Roy. Soc. London B* 315: 63–73.

Haszprunar, G. 1992. The first molluscs—small animals. *Boll. Zool.* 59: 1–16.

Heath, H. 1899. The development of *Ischnochiton. Zool. Jahrb., Anat.* 12: 567–656.

Heath, H. 1904. The nervous system and subradular organ in two genera of Solenogastres. *Zool. Jahrb., Anat.* 20: 399–408.

Heath, H. 1905. The morphology of a Solenogastre. *Zool. Jahrb. Anat.* 21: 703–734.

Heath, H. 1911. The Solenogastres. Reports on the scientific results of the expedition to the tropical Pacific . . . by the "Albatross" . . . *Mem. Mus. Comp. Zool.* (Harvard University) 45(1): 1–179.

Hessler, R. R., G. D. Wilson, and D. Thistle. 1979. The deep-sea isopods: a biogeographic and phylogenetic overview. *Sarsia* 64: 67–75.

Hoffman, S. 1949. Studien über das Integument der Solenogastren nebst Bemerkungen über die Verwandtschaft zwischen den Solenogastren und Placophoren. *Zool. Bidr. Uppsala* 27: 293–427.

Hoffmann, H. 1929–30. Aplacophora. Pp. 1–134, 383–453 in *Bronns Klassen und Ordnungen des Tier-Reichs*, Band III, Abt. I.

Hyman, L. H. 1967. *The Invertebrates.* Vol. VI. *Mollusca I* McGraw-Hill, Inc., New York. vii + 792 pp.

Ivanov, D. L. 1991. [Tentacular region of the central nervous system of the Mollusca and the homology of the organs of locomotion.] *Ruthenica* 1: 81–89. [In Russian]

Ivanova-Kazas, O. M. 1985a. Origin and phylogenetic significance of trochophore larvae. *Zool. Zhur.* 64(4): 485–497. [In Russian. English translation no. 1112119, National Museum of Canada, in manuscript.]

Ivanova-Kazas, O. M. 1985b. Origin and phylogenetic significance of trochophore larvae. *Zool. Zhur.* 64(5): 650–660. [In Russian. English translation no. 1112120, National Museum of Canada, in manuscript.]

Jägersten, G. 1947. On the structure of the pharynx of the Archiannelida with special reference to there occurring muscle cells of aberrant type. *Zool. Bidr. Uppsala* 25: 551–570.

Jägersten, G. 1963. On the morphology and behaviour of Pelagosphaera larvae (Sipunculoidea). *Zool. Bidr. Uppsala* 36: 27–35.

Jägersten, G. 1972. *Evolution of the Metazoan Life Cycle.* Academic Press, London and New York.

Kaiser, P. 1976. *Neomenia herwigi*, sp. n., ein bemerkenswerter Vertreter der Solenogastren (Mollusca, Aculifera) aus Argentinischen Schelfgewässern. *Mitt. Hamb. Zool. Mus. Inst.* 73: 57–63.

Kerth, K. 1983. Radulaapparat und Radulabildung der Mollusken. II. Zahnbildung, Abbau und Radulawachstum. *Zool. Jahrb., Anat.* 110: 239–269.

Kniprath, E. 1980. Ontogenetic plate and plate field development in two chitons, *Middendorffia* [= *Lepidochitona*] and *Ischnochiton. Wilhelm Roux's Arch. Devel. Biol.* 189: 97–106.

Kowalevsky, M. A. 1883. Embryogénie du *Chiton polii* Phil., avec quelques remarques sur le développement des autres Chitons. *Ann. Mus. Hist. Nat. Marseille* 1: 1–46.

Lake, J. A. 1990. Origin of the Metazoa. *Proc. Nat. Acad. Sci. USA* 87: 763–766.

Lemche, H., and K. G. Wingstrand. 1959. The anatomy of *Neopilina galatheae* Lemche, 1957 (Mollusca Tryblidiacea). *Galathea Rept.* 3: 9–71.

McKinney, M. L., and K. L. McNamara. 1991. *Heterochrony: the Evolution of Ontogeny.* Plenum Press, New York and London. xix + 437 pp.

Monniot, C., and F. Monniot. 1978. Recent work on the deep-sea tunicates. *Oceanogr. Mar. Biol. Ann. Rev.* 16: 181–228.

Moor, B. 1983. Organogenesis. Pp. 123–177 in *The Mollusca. Vol. 3, Development*, N. H. Verdonk, J. A. M. van den Biggelaar, and A. S. Tompa, eds. Academic Press, New York.

Newby, W. W. 1940. The embryology of the echiuroid worm *Urechis caupo. Mem. Am. Philos. Soc.* 16: 1–213.

Nielsen, C., and A. Norrevang. 1985. The trochaea theory: an example of life cycle phylogeny. Pp. 28–41 in *The Origins and Relationships of Lower Invertebrates. Syst. Assoc. Spec. Vol. No. 28*, S. Conway Morris, J. D. George, R. Gibson, and H. M. Platt, eds. Clarendon Press, Oxford.

Plate, L. H. 1898. Die Anatomie und Phylogenie der Chitonen. *Zool. Jahrb., Suppl. IV (Fauna Chilensis I)*: 1–243.

Raff, R. A., and T. C. Kaufman. 1983. *Embryos, Genes, and Evolution.* Macmillan Publishing Co., Inc., New York & Collier Macmillan Publishers, London.

Raven, C. P. 1966. *Morphogenesis: The Analysis of Molluscan Development.* 2nd ed. Pergamon Press, Oxford etc. xiii + 365 pp.

Reynolds, P. D., and M. P. Morse. 1991. Morphological evidence for ultrafiltration of blood in the Aplacophora. *Amer. Zool.* 31: 137A.

Rice, M. E. 1969. Possible boring structures of Sipunculids. *Amer. Zool.* 9: 803–812.

Rice, M. E. 1973. Morphology, behavior, and histogenesis of the pelagosphera larva of *Phascolosoma agassizii* (Sipuncula). *Smithsonian Contr. Zool.* 132: 51 pp.

Rice, M. E. 1975. Sipuncula. Pp. 67–127 in *Reproduction of Marine Invertebrates. Vol. 2. Entoprocts and lesser coelomates*, A. Giese, and J. Pearse, eds. Academic Press, New York.

Rice, M. E. 1981. Larvae adrift: Patterns and problems in life histories of sipunculans. *Am. Zool.* 21: 605–619.

Rice, M. E. 1985. Sipuncula: developmental evidence for phylogenetic inference. Pp. 274–296 in *The Origins and Relationships of Lower Invertebrates*, S. Conway Morris, J. D. George, R. Gibson, and H. M. Platt, eds. Oxford University Press, Oxford.

Runnegar, B., and J. Pojeta, Jr. 1985. Origin and diversification of the Mollusca. Pp. 1–57 in *The Mollusca, Vol. 10, Evolution*, E. R. Trueman, and M. R. Clarke, eds. Academic Press, Orlando, FL.

Salvini-Plawen, L. v. 1968a. Die 'Funktions-Coelom Theorie' in der Evolution der Mollusken. *Syst. Zool.* 17: 192–208.

Salvini-Plawen, L. v. 1968b. Über Lebendbeobachtungen an Caudofoveata (Mollusca, Aculifera), nebst Bemerkungen zum System der Klasse. *Sarsia* 31: 105–126.

Salvini-Plawen, L. v. 1972. Zur Morphologie und Phylogenie der Mollusken: Die Beziehungen der Caudofoveata und der Solenogastres als Aculifera, als Mollusca und als Spiralia. *Z. wiss. Zool.* 184: 205–394.

Salvini-Plawen, L. v. 1978. Antarktische und subantarktische Solenogastres (eine Monographie: 1898–1974). *Zoologica* 44: 1–315.

Salvini-Plawen, L. v. 1981a. On the origin and evolution of the Mollusca. *Att. Convegni Lincei* 49: 235–293.

Salvini-Plawen, L. v. 1981b. The molluscan digestive system in evolution. *Malacologia* 21: 371–401.

Salvini-Plawen, L. v. 1985. Early evolution and the primitive groups. Pp. 59–150 in *The Mollusca, Vol. 10. Evolution.* E. R. Trueman, and M. R. Clarke, eds. Academic Press, Orlando, FL.

Salvini-Plawen, L. v. 1990. Origin, phylogeny and classification of the phylum Mollusca. *Iberus* 9: 1–33.

Sanders, H. L., and J. A. Allen. 1973. Studies on deep-sea Protobranchia (Bivalvia); Prologue and the Pristiglomidae. *Bull. Mus. Comp. Zool.* 145: 237–262.

Scheltema, A. H. 1972. The radula of the Chaetodermatidae (Mollusca, Aplacophora). *Z. Morph. Tiere* 72: 361–370.

Scheltema, A. H. 1973. Heart, pericardium, coelomoduct openings, and juvenile gonad in *Chaetoderma nitidulum* and *Falcidens caudatus* (Mollusca, Aplacophora). *Z. Morph. Tiere* 76: 97–107.

Scheltema, A. H. 1978. Position of the class Aplacophora in the phylum Mollusca. *Malacologia* 17: 99–109.

Scheltema, A. H. 1981. Comparative morphology of the radula and alimentary tracts in the Aplacophora. *Malacologia* 20: 361–383.

Scheltema, A. H. 1985. The aplacophoran family Prochaetodermatidae in the North American Basin, including *Chevroderma n.g.* and *Spathoderma n.g.* (Mollusca: Chaetodermomorpha). *Biol. Bull.* 169: 484–529.

Scheltema, A. H. 1987. Reproduction and rapid growth in a deep-sea aplacophoran mollusc, *Prochaetoderma yongei. Mar. Ecol. Progr. Ser.* 37: 171–180.

Scheltema, A. H. 1988. Ancestors and descendents: relationships of the Aplacophora and Polyplacophora. *Amer. Malacol. Bull.* 6: 57–68.

Scheltema, A. H. 1990. Aplacophora as a Tethyan slope taxon: evidence from the Pacific. *Bull. Mar. Sci.* 47: 50–61.

Scheltema, A. H., K. Kerth, and A. M. Kuzirian. 1989. The primitive molluscan radula. P. 220 in *Unitas Malacologica 10th International Congress*, Tübingen. [Abstract]

Scheltema, A. H., and A. M. Kuzirian. 1991. *Helicoradomenia juani* n.g. n. sp., a Pacific hydrothermal vent Aplacophora (Mollusca, Neomeniomorpha). *Veliger* 34: 195–203.

Scheltema, A. H., M. Tscherkassky, and A. M. Kuzirian. (In press). Aplacophora. In *Microscopic Anatomy of Invertebrates. Vol. 5. Mollusca: Monoplacophora, Aplacophora, Polyplacophora, and Gastropoda*, F. W. Harrison and A. J. Kohn, eds. Wiley-Liss, New York.

Soetaert, K., and C. Heip. 1989. The size structure of nematode assemblages along a Mediterranean deep-sea transect. *Deep-Sea Res.* 36: 93–102.

Spengel, J. W. 1881. Die Geruchsorgane und das Nervensystem der Mollusken. *Z. wiss. Zool.* 35: 333–383.

Tendal, O. S. 1985. Xenophyophores (Protozoa, Sarcodina) in the diet of *Neopilina galatheae* (Mollusca, Monoplacophora). *Galathea Rept.* 16: 95–98.

Thiele, J. 1902. Die systematische Stellung der Solenogastren und die Phylogenie der Mollusken. *Z. wiss. Zool.* 72: 249–466.

Tscherkassky, M. 1989. Pedal shield or oral shield in Caudofoveata (Mollusca, Aculifera)? P. 254 in *Unitas Malacologica, Abstracts of 10th International Malacological Congress*, Tübingen. [Abstract]

Turbeville, J. M. 1986. An ultrastructural analysis of coelomogenesis in the hoplonemertine *Prosorhochmus americanus* and the polychaete *Magelona* sp. *J. Morphol.* 187: 51–60.

Turbeville, J. M., K. G. Field, and R. A. Raff. 1992. Phylogenetic position of phylum Nemertini, inferred from 18S rRNA sequences: molecular data as a test of morphological character homology. *Mol. Biol. Evol.* 9: 235–249.

van Dongen, C. A. M., and W. L. M. Geilenkirchen. 1974. The development of *Dentalium* with special reference to the significance of the polar lobe. I, II and III. Division chronology and development of the cell pattern in *Dentalium dentale* (Scaphopoda). *Proc. K. Nederl. Akad. Wetens.*, ser. C, 77: 57–100.

Verdonk, N. H., and J. A. M. van den Biggelaar. 1983. Early development and the formation of the germ layers. Pp. 91–122 in *The Mollusca. Vol. 3. Development*, N. H. Verdonk, J. A. M. van den Biggelaar, and A. S. Tompa, eds. Academic Press, New York.

Watters, G. T. 1991. Utilization of a simple morphospace by polyplacophorans and its evolutionary implications. *Malacologia* 33: 221–240.

Westheide, W. 1987. Progenesis as a principle in meiofauna evolution. *J. Nat. Hist.* 21: 843–854.

Wettstein, E. 1904. Anatomie von Cryptoplax. *Jenaische Z. Naturwiss.* 38: 473–504.

Whittington, H. B. 1985. *The Burgess Shale.* Yale University Press, New Haven and London. xv + 151 pp.

Willmer, P. G., and P. W. H. Holland. 1991. Modern approaches to metazoan relationships. *J. Zool., London,* 224: 689–694.

Wilson, E. B. 1892. The cell-lineage of Nereis. *J. Morphol.* 6: 361–480.

Wingstrand, K. G. 1985. On the anatomy and relationships of Recent Monoplacophora. *Galathea Rept.* 16: 7–94.

Wissel, C. v. 1904. Pacifische Chitonen. *Zool. Jahrb., Syst.* 20: 591–676.